Semantic Language in the Right Hemisphere:

Divided Visual Field and Functional Imaging Studies of Reading

Thesis

presented to the Faculty of Arts

of the University of Zurich

for the degree of Doctor of Philosophy

by

Kirsten I. Taylor Monsch

of Hayward, California, United States of America

accepted on the recommendation of

Professor Marianne Regard, Ph.D.

Zürich, December 2002

for Karin and Mike

Preface

The research reported here was conducted at the Neuropsychology Unit of the Neurology Clinic at the University Hospital Zürich. I am indebted to Professor Dr. phil. Marianne Regard, PD Dr. phil. II Peter Brugger and Dr. phil. Dorothea Weniger, whose neurolinguistic expertise was especially helpful, for their constant support and guidance through all phases of the dissertation. I also thank Yvonne Döbeli for her administrative help, Enrique Wintsch for his technical support and Marco Tettamanti for his assistance with the post-processing of the functional imaging data, as well as all the healthy participants of the studies reported here. I gratefully acknowledge the generous support of the following foundations which have made this research possible: the Betty and David Koetser Foundation for Brain Research, the Roche Research Foundation and the Hartmann-Müller Foundation. Finally, I thank PD Dr. phil. Andreas Monsch for his continuous support.

The studies presented here represent the joint efforts of the research group at the USZ Neuropsychology Unit (Prof. Dr.phil. M. Regard, PD Dr.phil. II P. Brugger and Dr.phil. D. Weniger) and, in the functional imaging study, the USZ Department of Neuroradiology. I am especially grateful for the support provided by PD Dr.med. S. Kollias, director of the functional imaging facilities, and Dr.phil. G. Crelier and Dr.med. H. Alkadhi from the Department of Neuroradiology, without which the functional imaging study presented here would not have been possible. Drs. Klemens Gutbrod and Katrin Henke provided comments very helpful to study 3.2., and study 3.3. was inspired by Professor Agnes Chan's work with Professor David Salmon and the late Professor Nelson Butters at the University of California at San Diego.

Table of Contents

List of Figures

List of Tables

1. Abstract

English Abstract

A long-standing neurological maxim posits that the left cerebral hemisphere (LH) is the sole organ of language. This conception had to be amended, however, to account for the findings from callosotomy patients and the ensuing research with unilaterally brain-damaged patients and divided visual field studies with healthy subjects. These suggested that the right hemisphere (RH) significantly participates in language processing, in particular at the conceptual (semantic) level. The studies reported here investigated three aspects of RH semantic language ability: 1) the influence of task demands on measures of RH semantic competence; 2) the functional neuroanatomical contribution of the RH to "pure" semantic processing; and, 3) qualitative aspects of RH semantic processing. The results of the first study revealed comparable hemispheric competence for semantic processing in terms of reaction times when an explicit semantic decision, but not when an implicit semantic decision, was required. In the second, functional MRI study, the LH was found to be functionally dominant during lexical processing, but functional dominance shifted to the RH during pure semantic processing. While both hemispheres appear competent to process semantic information, the findings of the final study suggest that they do so in qualitatively different ways: the LH may focally activate the semantic network, while RH activation may be more diffuse, coactivating more distantly related concepts. The relevance of these findings for aphasia therapy programs and their implications for metaphor comprehension, the concept of creativity and paranormal and psychotic thought are discussed.

Deutsches Abstrakt

Eine seit langem bestehende Maxime in der Neurologie besagt, dass die linke Hemisphäre (LH) das alleinige Organ für die Sprache ist. Diese Vorstellung wurde inzwischen aufgrund der Befunde bei Kallosotomiepatienten, den Forschungsarbeiten bei unilateral hirngeschädigten Patienten und bei Gesunden, verlassen. Diese Befunde wiesen nämlich darauf hin, dass die rechte Hemisphäre (RH) insbesondere inbezug auf die Semantik einen wesentlichen Beitrag bei der Sprachverarbeitung leistet. In der hier beschriebenen Arbeit wurden drei Aspekte dieser Fähigkeit untersucht: 1) der Einfluss des Anforderungstypes einer Aufgabe auf die RH-semantischen Kompetenz; 2) den funktionellen neuroanatomischen Beitrag der RH zur "reinen" semantischen Verarbeitung; und, 3) qualitative Aspekte der RH-semantischen Verarbeitung. Die Resultate der ersten Studie zeigten, dass bei explizit (aber nicht implizit) semantischen Entscheidungsaufgaben beide Hemisphären vergleichbare Kompetenz aufwiesen. In der zweiten, fMRI Studie, zeigte sich eine LH funktionelle Aktivität für die lexikalische Verarbeitung, die sich aber für die reine semantische Verarbeitung zugunsten der RH verschob. Während beide Hemisphären sich als semantisch kompetent erwiesen, deuteten die Befunde der dritten Studie darauf hin, dass sie diese auf qualitativ unterschiedliche Weise erbringen: die LH aktiviert das semantische Netzwerk eher fokal, die RH eher diffus, sodass entfernt verwandte Konzepte mitaktiviert werden. Die Relevanz dieser Befunde für Therapieprogramme mit aphasischen Patienten, sowie deren Implikationen für das Metapherverständnis, für das Konzept der Kreativität und für paranormales und psychotisches Denken, werden diskutiert.

2. General Introduction

2.1. Historical Background

Figure 1. Philippe Pinel (1745-1826) with patients in the courtyard of the mental institution Salpêtrière (from Finger, 1994, p. 390).

The association between left hemisphere (LH) lesions and aphasia has been recognized since antiquity. Still, until the end of the 19th century, patients who had lost the ability to speak were considered mentally ill and confined to psychiatric institutions (Figure 1). Such a patient was sent to the French surgeon, Paul Broca, in 1861 for treatment of gangrene. For twenty years this patient's utterances had been restricted to various expletives[1] and the syllable 'Tan', which Broca adopted as the patient's name.

[1] These have been omitted from neuropsychology textbooks. See Van Lancker and Cummings (1999) for a comprehensive review of the neuropsychology of expletives.

Tan died shortly afterwards, providing Broca with the opportunity to autopsy his brain (Figure 2). He associated the area of damage he found restricted to Tan's left inferior frontal lobe with capacity for articulate speech[2] and became the unwilling spokesperson for a necessarily localizationist stance in the post-Gallian era. Supported by Wernicke's association of *Klangbilder* with the left superior posterior temporal lobe (Wernicke, 1874) and Déjérine's recognition of alexia with agraphia subsequent to left angular gyral damage (Déjérine, 1891), a preeminent role of the LH in language processing was inexorably established.

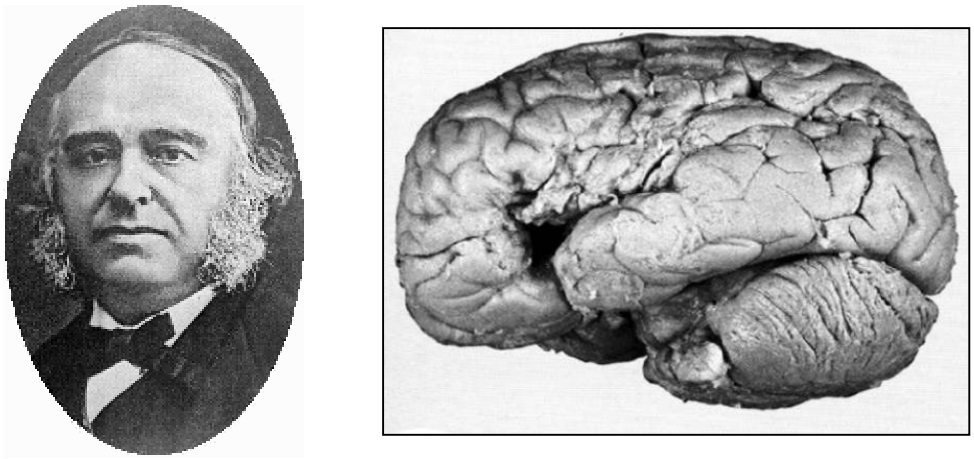


Figure 2. The french surgeon Paul Broca (left) and Tan's autopsied brain (right).

It was at this time that John Hughlings Jackson (Figure 3) argued for temperance. According to Jackson, Broca had established a role of the left inferior frontal lobe in *articulate language*, not language *per se* (Finger, 1994). Significantly, Jackson's differentiated conception of the functional neuroanatomy of language included an important role of the hemisphere (RH). This idea was in part reached, ironically, through his careful observations of the spared language abilities of such

[2] Marc Dax had presented a summary of over forty such similar cases of LH lesions, aphasia and right hemiplegia in a paper read at the *Congrès Méridional de Montpellier* in 1836. This paper was first sent to

aphasic patients as Tan, i.e. the "automatic" utterances of emotional expletives, words which could not be voluntarily repeated by the same patient upon command: "The right hemisphere is the one for the most automatic use of words, and the left the one in which automatic use of words merges into voluntary use of words - into speech" (Jackson, 1874). According to Jackson, the RH not only played a role in automatic language, but shared the ability of the LH to learn and comprehend speech (Jackson, 1873). Unfortunately, Jackson's ideas were largely overlooked amidst the 19th century conceptual struggle against an apparent phrenological regression (Harrington, 1987). The general neurological maxim which emerged conceptualized a "dominant" hemisphere as synonymous with the LH at the expense of the hemispheric balance of function championed by Jackson.

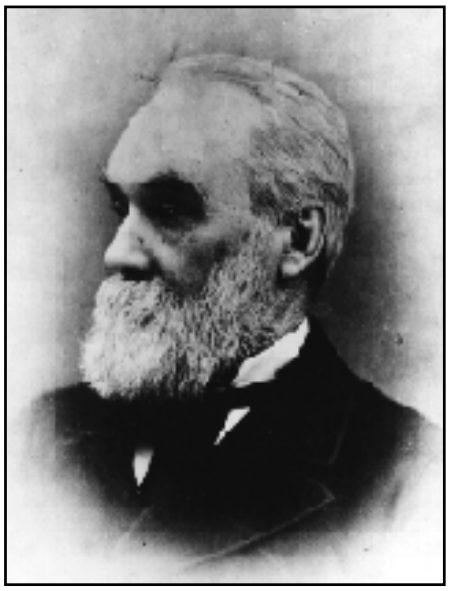


Figure 3. John Hughlings Jackson (1835-1911).

2.2. RH Language in the 20th Century

This maxim was fundamentally challenged nearly a century later by behavioral studies with callosotomy patients (Sperry, 1961), studies for which the principal investigator later received the Nobel Prize, the first and to date only Nobel Prize rewarded to a psychologist. Although devoid of naming (articulatory) ability, the disconnected RHs proved their written and auditory word comprehension by e.g. selecting with their left hand the appropriate object from among an array (see Figure 4;

---

the Parisian *Académie de Médecine* by his son Gustave Dax in 1863 (Finger & Roe, 1996).

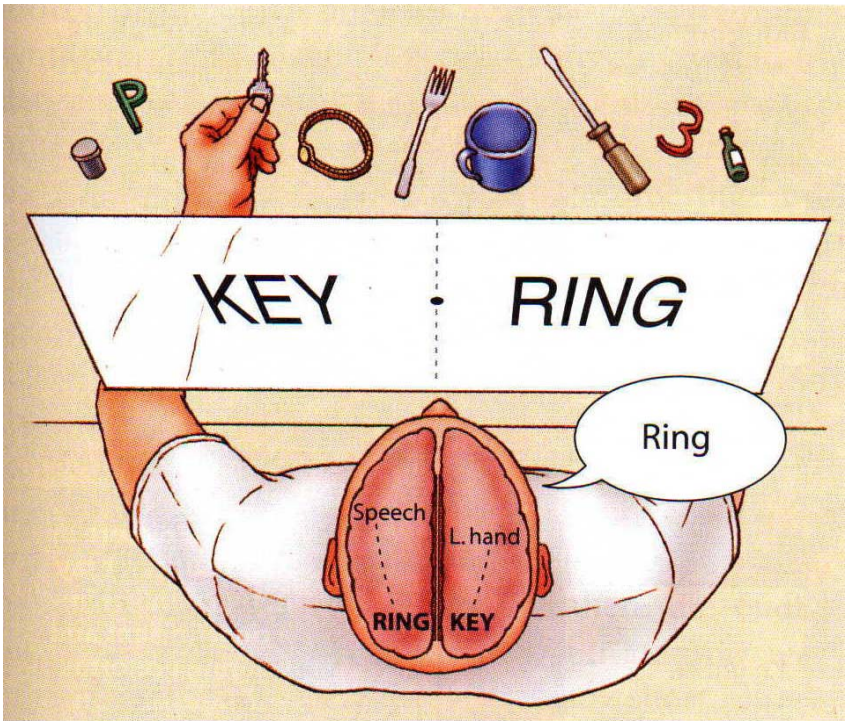


Figure 4. Experimental procedure employed with callosotomy patients (Gazzaniga, Ivry & Mangun, 1998, p. 331).

Gazzaniga & Sperry, 1967). The disconnected RHs also demonstrated competence for semantic (matching printed synonyms and antonyms (Zaidel, 1982); appreciation of superordinate-subordinate and functionality relationships (Zaidel, 1978); facilitated lexical decisions with semantically related auditory primes (Zaidel, 1983)) and ideational tasks (i.e. abstraction, generalization, and mental association; Gazzaniga & Sperry, 1967). Despite the methodological and interpretational critiques forwarded against these findings (Sperry, 1982; Gazzaniga, 1983)[3], they nevertheless demonstrated fundamental RH language abilities. Based on the model of written word comprehension and repetition shown in Figure 5, the comprehension ability evidenced by disconnected RHs demonstrated that the RH was capable of orthographic analysis and possessed an orthographic input lexicon (see also Coltheart, 1980, for a discussion of the role of the

RH in deep dyslexia, and Landis, Regard & Serrat, 1980) and semantic system. The RH's inability to name written words, on the other hand, indicated a lack of a

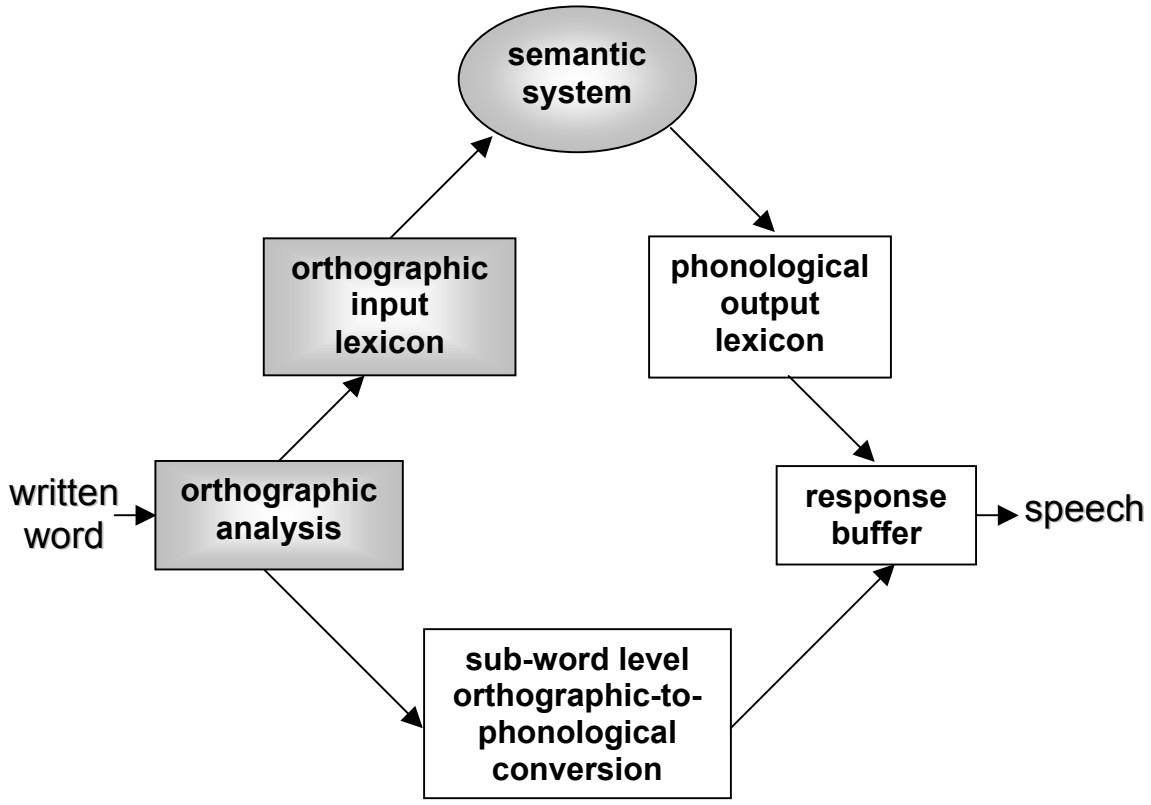


Figure 5. Model of written word processing. The component language processes for which the RH is presumed competent are shown in gray (adapted from Coltheart, 1987, p. 6).

phonological output lexicon and response buffer as well as the inability to perform sub-word level orthographic-to-phonological conversions. These findings thus mirror Jackson's proposal of bilateral receptive and unilateral (LH) expressive language abilities in the written verbal modality (Jackson, 1873).

An alternative approach to the study of RH language competence is to investigate which language abilities are spared and which impaired in unilaterally brain-damaged patients. For example, Winner and Gardner (1977) read metaphoric

---

[3] E.g., it is unclear whether and if, to what extent long-term epilepsy leads to atypical (bilateral) language representation, patients may differ with respect to the nature of the epileptogenic lesion (e.g. constitutional or overt cerebral pathology) and the nature of the surgery (e.g. partial vs. complete resection of the corpus callosum), and other modes of information transfer cannot always be ruled out (e.g. spared anterior commissures, subcortical structures and cross-cueing strategies).

sentences to LH and RH unilaterally brain-damaged (LHD and RHD, respectively) patients, demented subjects and normal controls and instructed them to choose one of four pictures which best represented the sentence. The picture either illustrated the 1) metaphoric or 2) literal meaning of the sentence, or depicted an 3) adjective or 4) noun in the sentence. Adjective and noun sentences were rarely chosen by all groups, and significant differences were restricted to the proportion of metaphor and literal pictures chosen. Whereas the LHD patients (as well as the control subjects) chose significantly more metaphoric sentences compared to the RHD patients, the RHD patients chose significantly more literal sentences compared to the LHD patients and control subjects

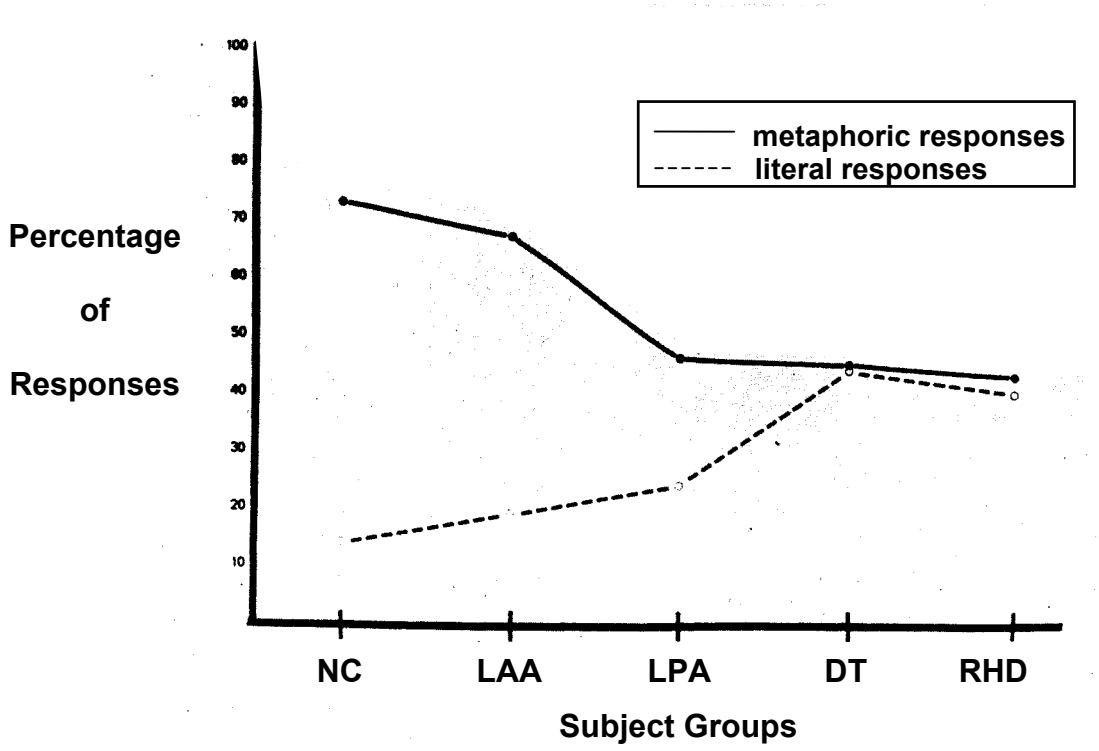


Figure 6. Percentage of metaphoric and literal responses of the normal control group (NC) and left anterior and posterior aphasic (LAA and LAP, respectively), demented (DT) and RH brain-damaged patients on the picture-metaphor test (adapted from Winner & Gardner, 1977, p. 722).

(see Figure 6). These results indicated that while the LHD patients appreciated the metaphoric meaning of the sentences, the RHD patients did not. Thus, Winner and Gardner (1977) succeeded in describing a high-level language ability for which the RH

appeared to be especially important. These findings have since been replicated and extended, in particular by the Brownell group (Brownell, Potter & Michelow, 1984; Brownell, 1988; Brownell, Simpson, Bihrle, Potter & Gardner, 1990). The comprehension of figurative, metaphoric language, however, requires a lower-level, conceptual system to support it. Further research with unilaterally brain-damaged patients thus proceeded from a high (metaphoric) -to-low (semantic) level search of RH language ability, in contrast to research with callosotomy patients, which next concentrated on specific semantic impairments in RHD patients.

Various deficits in semantic processing have indeed been demonstrated in RHD patients. Glosser and Goodglass (1991) reported that RHD patients made more idiosyncratic or totally unrelated responses to single oral word associations. Villardita et al. (1988) found that RHD patients exhibited a semantic clustering deficit for concrete but not abstract words in free recall portions of their verbal learning task. Similarly, right temporal lobectomy patients were incapable of utilizing category membership in recall portions of a verbal memory task of concrete words, whereas left temporal lobectomy patients could (Channon, Daum & Polkey, 1989), and RHD, but not LHD, patients displayed deficits in categorizing pictures of familiar objects (Incisa della Rocchetta, 1986, but see Grossman & Wilson, 1987). Finally, Joanette and Goulet (1986) demonstrated that RHD patients were overproportionally impaired on semantic, but not phonemic, fluency (i.e. the production of words beginning from a given category or with a given first letter, respectively) compared to control subjects (see also Varley, 1995, and Martin, Loring, Meador & Lee, 1990).

Neuropsychological investigations with patients who underwent callosotomy or suffered unilateral brain damage thus indicate that the RH possesses lexical, semantic and metaphoric language abilities. Replication studies with healthy subjects, however,

are critical to rule out the possibility that these functions are not merely the result of developmental and/or post-morbid plastic changes in the language system. The method most commonly employed to study hemispheric language abilities in healthy subjects is to induce an "experimental split-brain" with divided sensory-field (auditory or visual) experiments (see Figure 7).

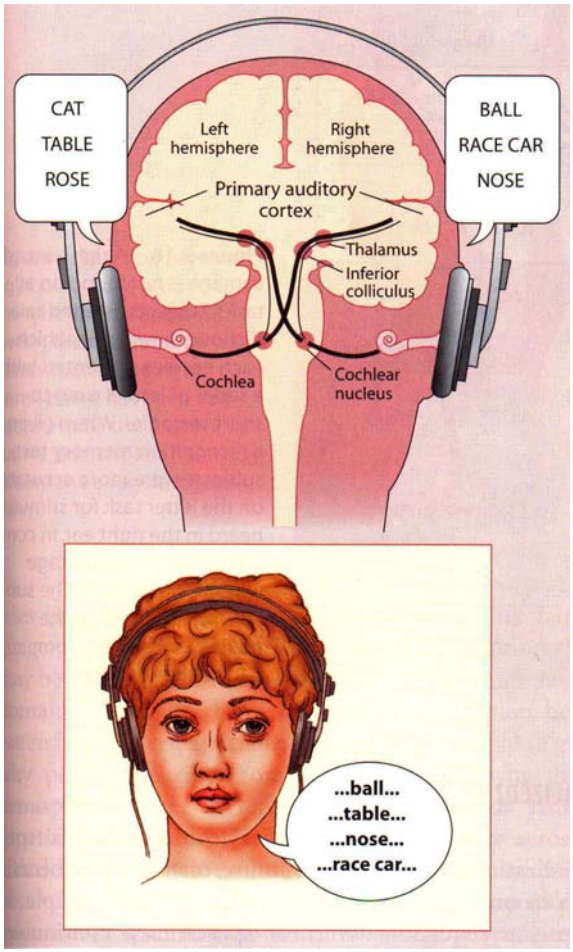
Shepherd Ivory Franz, director of UCLA's Department of Psychology from 1925 until his death in 1933, was the first to conduct psychological experiments on the nature of hemispheric specialization in normal people (Gold, 1997) using a split visual field, tachistoscopic design[4] (Zaidel, 1983). It was not until twenty years later, however, that Mishkin and Forgays of McGill University reported the since celebrated finding of a right visual field (RVF) naming advantage for horizontally presented words (Mishkin & Forgays, 1952)[5].

The procedure of split-visual field experiments has since become a standard for the investigation of written language ability in the LH and RH (Hellige, 1983). The visual modality is preferable to the auditory modality, which sends fibers also to ipsilateral sites (Springer & Deutsch, 1998). Consistent RVF/LH advantages are achieved with the lexical decision paradigm (i.e. deciding whether a letter string represents a real word or not), indicating that the processing of the orthographic input lexicon (see Figure 5) is superior in LH.

---

[4] Franz's first experiment presented healthy subjects with words split across the visual field (i.e. first half in left visual field (LVF), second half in right visual field (RVF)) for 100 msec. The superior LVF performance which emerged was interpreted as a RH advantage for the task (Franz & Davis, 1933, cited in Zaidel, 1983), although the left-to-right scanning induced by the task (i.e. the reading of the leftmost letters first) most likely accounted for LVF advantage (Zaidel, 1983).

[5] Eran Zaidel, upon his arrival as a faculty member at UCLA, delivered a talk in which he asserted that Mishkin and Forgays were the first to conduct a study on the nature of hemispheric specialization in healthy subjects. An older professor from the audience corrected Zaidel: "Franz did it first". When Zaidel asked "Who is Franz?", the professor replied, "Franz is the man after whom this building is named!"(Gold, 1997).



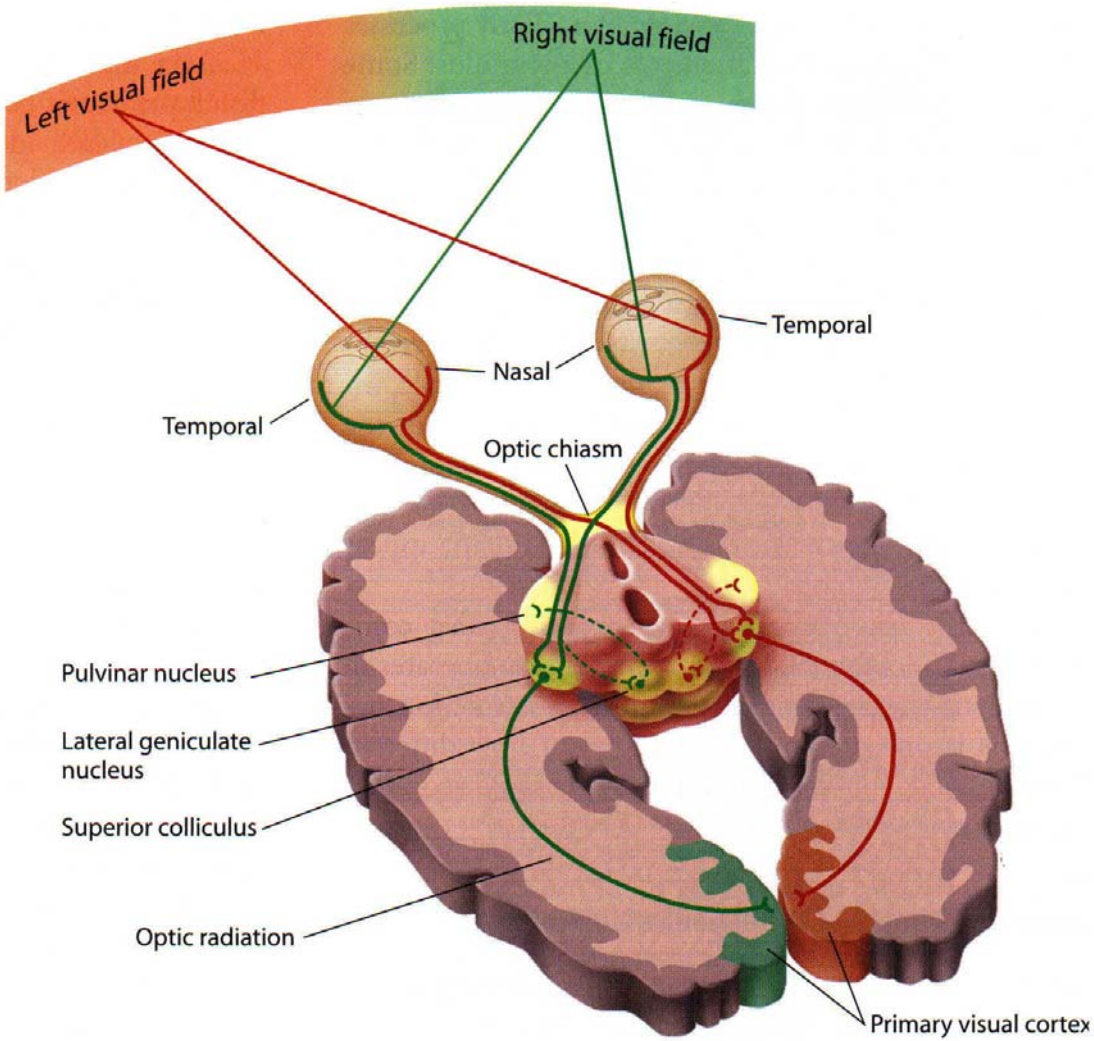


Figure 7. Dichotic listening experiment (left; Gazzaniga, Ivry & Mangun, 1998, p. 343) and hypothesized flow of visual information in the tachistoscopic split visual field task (right).

Semantic processing capacities of the LH and RH have also been studied with split visual field methodology. Two approaches have generally been adopted. The first presents a lateralized lexical decision task with stimuli *a priori* grouped into different semantic classes (e.g. concrete vs. abstract, high vs. low imageability). The visual field/hemisphere with the superior performance for a given semantic class is presumed to preferentially store or process this semantic information (Hines, 1976; Jackman, 1985; McMullen & Bryden, 1987; Koenig, Wetzel & Caramazza, 1992). The second

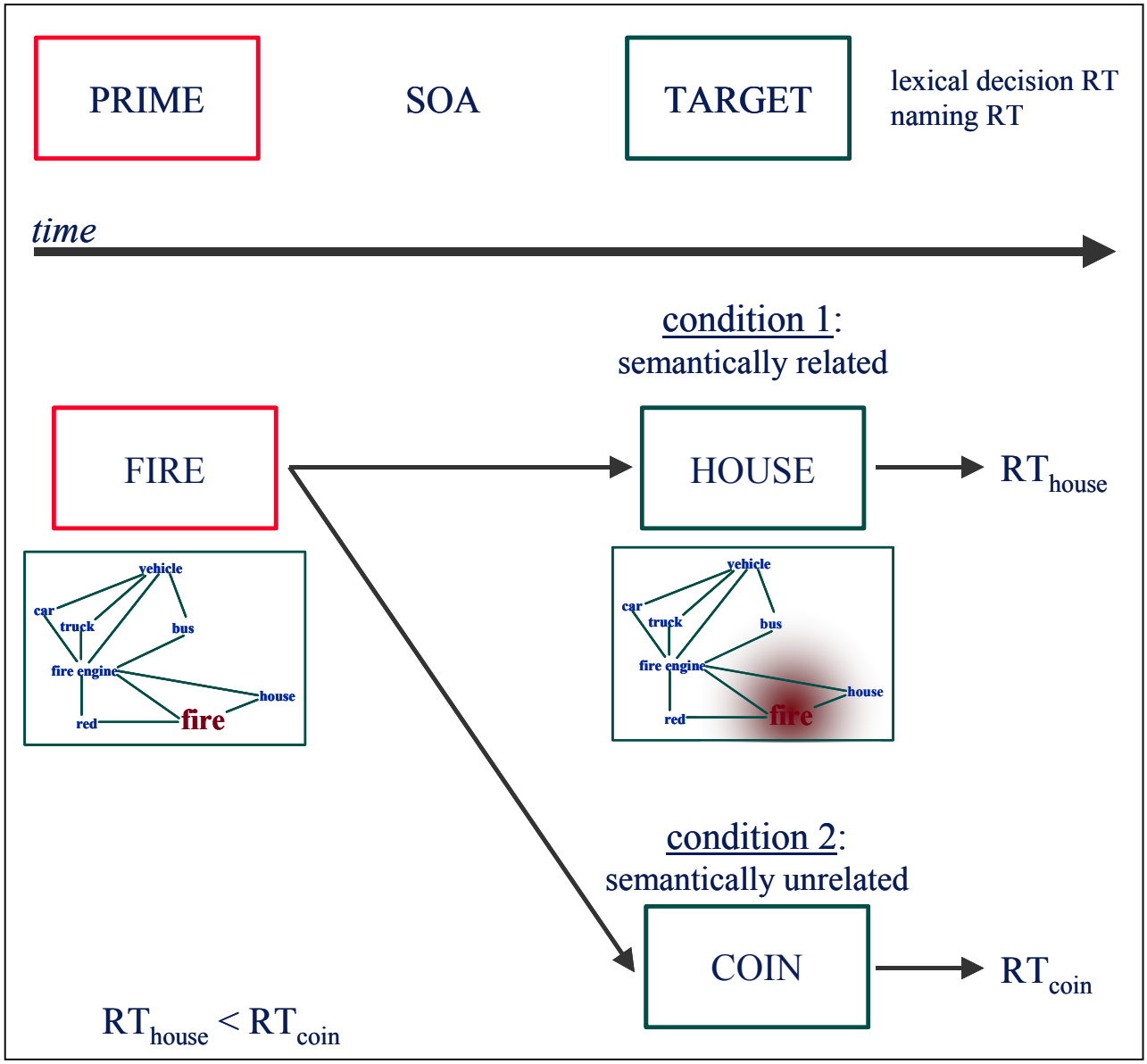


Figure 8. Experimental design and theoretical foundations of the priming paradigm, where SOA = stimulus onset asynchrony, RT = reaction time, and facilitation is defined as $[RT_{unrelated}] - [RT_{related}]$; see text for details.

approach is the semantic priming of lexical decisions (see Figure 8). These studies presume that the activation arising from the presentation of the prime word spreads through links in the semantic network to related concepts during the stimulus onset asynchrony (SOA; i.e., the duration of time between presentation of prime and target stimuli; Collins & Loftus, 1975). If a semantically related target word has been reached by spreading activation by the time the target word is presented, the threshold for a response, and thus reaction time (RT), is reduced (Meyer & Schvaneveldt, 1971; Neely, 1976). Thus, if lexical decisions in a given hemifield are semantically primed and thus facilitated, then the semantic relationship is presumably represented in the corresponding hemisphere (e.g. Chiarello, Senehi & Nuding, 1987; Chiarello, Burgess, Richards & Pollock, 1990; Abernethy & Coney, 1996).

Both approaches described above do not explicitly require the retrieval of semantic information, an operation considered by some to be a defining characteristic of semantic memory (Warrington, 1975). The validity of generalizing results on semantic processing obtained with implicit semantic tasks to explicit semantic processing has not yet been ascertained. Moreover, during the SOA in divided-visual field priming experiments, the prime word becomes available to both hemispheres such that the opposite hemisphere can contribute or interfere with the lexical decision (Zaidel, White, Sakurai & Banks, 1988). To circumvent these drawbacks, semantic processing capacities of the hemispheres should be investigated with explicit semantic tasks[6].

---

[6] Explicit semantic tasks, e.g. semantic membership decisions (deciding whether the presented exemplar belonged to the presented superordinate category) and semantic matching decisions (deciding whether two exemplars belonged to the same semantic category), have been administered in divided visual field studies (Gross, 1972; Day, 1977; Urcuioli, Klein & Day, 1981). However, these studies always presented one stimulus foveally, i.e., to *both* hemispheres, such that the contribution or interference of the opposite hemisphere cannot be ruled out. Indeed, in a priming study, central-lateral presentations resulted in different hemispheric patterns of performances on semantic priming tasks compared to lateral-lateral presentations, such that the authors concluded that a more valid measure of hemispheric language ability may be achieved with fully lateralized, and not partially centralized, presentations (Chiarello, Burgess, Richards & Pollock, 1990).

2.3. Research Studies

2.3.1. A Split Visual Field Experiment of Implicit and Explicit Hemispheric Semantic Processing

The first study presented here (Study 3.1.) was designed to determine the effect of task demands - implicit vs. explicit semantic processing demands - on hemispheric patterns of semantic activation (Taylor, Weniger, Regard & Brugger, 2000; Taylor, Brugger, Weniger & Regard, submitted). Two divided-visual field (non-priming) paradigms were constructed: a unilateral lexical decision task (LDT) and a unilateral semantic decision task (SDT; specifically, a category matching task, i.e. deciding whether two target words belong to the same category). Importantly, the target stimuli in both tasks were identical: closely or distantly semantically related category exemplars. These stimuli were chosen since it had previously been demonstrated that RTs to closely related category exemplars are significantly faster than to those distantly related (semantic distance effect; Rips, Shoben & Smith, 1973; Caramazza, Hersh & Torgerson, 1976), an effect which reflects the appreciation of this semantic information. Thus, we planned to determine and compare the existence and extent of semantic distance effects (semantic processing) in the LH and RH under implicit (LDT) and explicit (SDT) semantic processing conditions.

The results of Study 3.1. demonstrated that, overall, the LH was more efficient than the RH in making lexical decisions. Both hemispheres, however, made semantic decisions equally quickly. Moreover, the stimuli's semantic content was not appreciated in either hemisphere in the implicit semantic condition (lexical decision task), whereas the semantic information was processed in *both hemispheres* to the *same extent* in the explicit condition (semantic decision task).

2.3.2. A Quantitative Functional Magnetic Resonance Imaging Study of Hemispheric Contributions to "pure" Semantic Processing

The findings described above as well as those from neuropsychological studies with neurological patients indicate that the RH is competent to process semantic information. Although the functional neuroanatomical characterization of the healthy RH conceptual system would have both weighty theoretical and clinical (i.e. neurorehabilitative) consequences, the anticipated contributions from functional imaging studies have not yet been forthcoming. These have typically employed two types of subtraction strategies to target lexicosemantic processing: the subtraction of activations during complex visual or during phonological baseline tasks from those tasks. The activated cortical regions in both approaches (Pugh, Shaywitz et al., 1996; Beauregard, Chertkow et al., 1997; Rumsey, Horwitz et al., 1997; Mummery, Patterson, Hodges & Price, 1998; Poldrack, Wagner et al., 1999) or completely isolated to LH cortical regions (Howard, Patterson et al., 1992; Vandenberghe, Price, Wise, Josephs & Frackowiak, 1996; Price, Moore, Humphreys & Wise, 1997; Rumsey et al., 1997; see Figure 9).

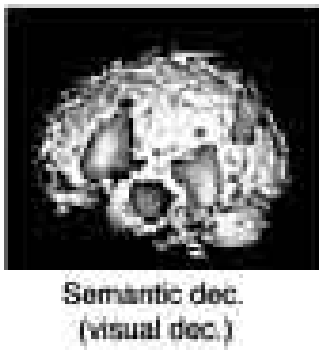


Figure 9. Review graphic of functional activations during visual semantic decisions (Price, 1998, p. 282).

The surprisingly minimal or complete lack of RH cortical activation may be the consequence of subtraction methodologies which extracted combined lexical *and* semantic processes and thus disadvantaged the lexically less competent RH. Furthermore, the region of interest analysis frequently employed in functional neuroimaging studies is founded on homotopic organizational principles, i.e. the assumption that if the hemispheres possess functionally equivalent abilities, that these are localized at mirror image sites. However, basic language functions in the RH may

be more diffusely organized (Semmes, 1968), as suggested by clinical findings that lesions sites leading to specific deficits of basic speech acts are much more widely distributed in the RH than in the LH (Zaidel, Kasher et al., 2000; see Figure 10).

The purpose of the second study (Study 3.2.) was to quantify each hemisphere's functional contribution to pure semantic processing (i.e., minimizing lexical processing; Taylor, Crelier et al., 2001; Taylor, Crelier et al., submitted). Three series of functional MRI tasks were employed. Each was designed with a unique orthographic, lexical and semantic paradigm. We planned to target lexical processes by subtracting activations

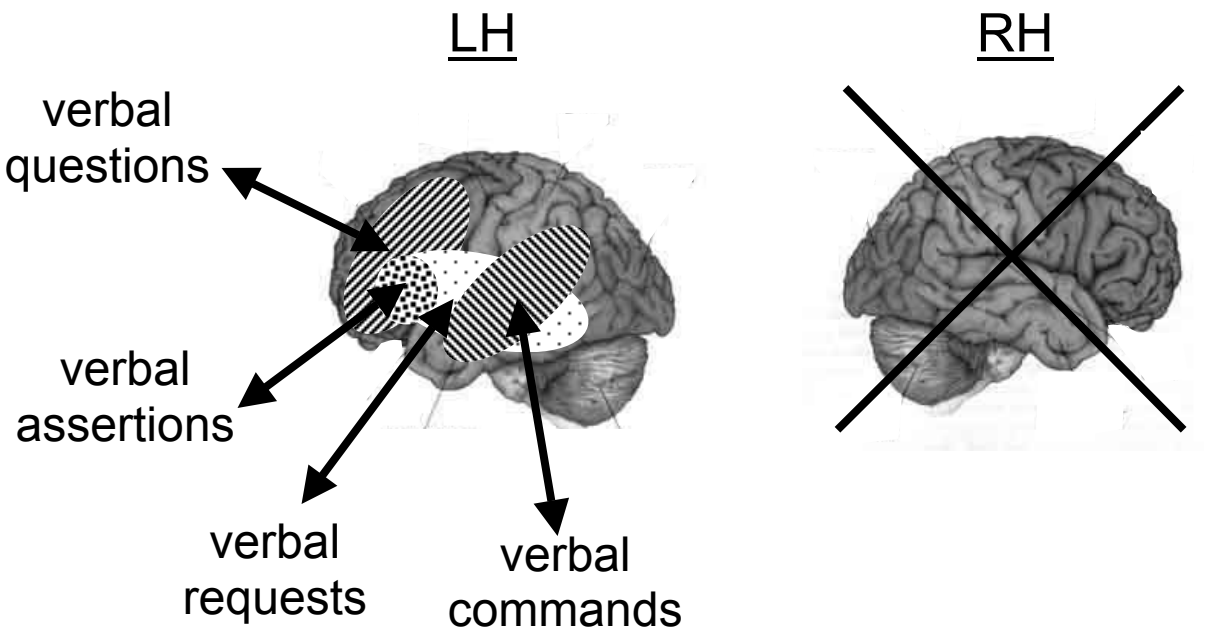


Figure 10. Depiction of correlation between deficits on basic speech acts and lesion site in LH and RH brain-damaged individuals.

during orthographic from those during lexical tasks ("pure" lexical processing), and to target semantic processes by subtracting activations during lexical from those during semantic tasks ("pure" semantic processing). The findings revealed the expected LH functional dominance for "pure" lexical processing and a shift to RH functional dominance for "pure" semantic processing. Thus, the RH appears to significantly participate in language processing at the semantic level.

2.3.3. Quality, and not Quantity: A Final Divided Visual Field Study of Qualitative Aspects of Hemispheric Semantic Processing

The first two studies investigated the *quantitative* nature of RH semantic processing. The third and last study presented here (Study 3.3.) focused on *qualitative* aspects of semantic processing in the hemispheres (Taylor, Regard & Brugger, 1998; Taylor, Brugger, Weniger & Regard, 1999). Two main theories have been forwarded to describe the different patterns of hemispheric performances on divided visual field priming studies of lexical decisions and naming RTs. The depth of activation hypothesis postulates that the LH rapidly and focally activates the semantic network whereas RH activation is slow and diffuse (i.e. although slow, it incorporates both closely and distantly related information; Chiarello, Burgess, Richards & Pollock, 1990; Beeman, Friedman et al., 1994). The time-course hypothesis of hemispheric semantic processing (Burgess & Simpson, 1988; Koivisto, 1997), on the other hand, is based on divided visual field priming studies which varied the duration of the SOA to determine "early" and "late" components of spreading activation in the semantic network. It postulates that both closely and distantly semantically related information are initially available to both hemispheres, but that later in the time course of semantic activation distantly related information is suppressed in the LH.

The development of theories of hemispheric processing based on divided visual field priming studies of lexical decisions and/or naming RTs, however, has two major drawbacks: 1) direct, explicit measures of semantic processing may offer a more realistic measure of semantic processing than those that are indirect and implicit (i.e. lexical decisions, naming RTs), and 2) the prime word becomes available to both hemispheres during the SOA such that the opposite hemisphere may contribute to or interfere with the hemisphere processing the target word (Zaidel, White, Sakurai &

Banks, 1988). A more direct and valid measure of hemispheric semantic competence is an explicit semantic task presented in a non-priming, unilateral[7] divided visual field paradigm. Study 2.3. therefore unilaterally presented target words to participants for a semantic decision (matching) task. It is well known that semantic decisions to simultaneously presented stimuli are faster when the stimuli are closely semantically related than when they are distantly semantically related (e.g. Rips, Shoben & Smith, 1973), an effect interpreted as the benefit from automatic spreading semantic activation for concepts more closely related in the semantic network than those more distantly related (Collins & Loftus, 1975). Qualitative hemispheric differences in semantic processing could thus be construed from each hemifield's RT patterns: a depth of activation performance pattern (i.e. focal LH and diffuse RH activation) would be reflected in consistently faster RTs to some (closely related) stimuli compared with others (distantly related) only in the left visual field/RH, whereas according to the time-course hypothesis, these systematic differences would be evidenced either in both visual fields or the right visual field/LH alone. The results, as described in detail in Study 3.3., support the depth of activation hypothesis of hemispheric semantic processing.

---

[7] See Boles (1990), Mohr, Pulvermüller, Rayman and Zaidel (1994) and Olk and Hartje (2001) for the effects of bilateral displays.

3. Own Contributions

Study 3.1. The Hemisphere's Semantic Response depends on the Question Asked

3.1.1. Abstract

Divided-visual field lexical decision tasks (LDTs) are often employed to measure each hemisphere's capacity to process semantic information. These lexical tasks thus yield *implicit* measures of semantic processing. Quantitatively and qualitatively different patterns of hemispheric semantic activation may result from tasks *explicitly* requiring the retrieval of semantic information (semantic decision tasks, SDTs). We administered unilateral lexical (implicit) and semantic (explicit) decision tasks to a group of healthy participants. Semantic processing was assessed by capitalizing on the known RT advantage for closely as opposed to distantly related categorical stimuli (semantic distance effect). Target word pairs were thus *a priori* dichotomized along this dimension and were identical in both tasks. In the LDT right visual field (RVF)/LH RT performances were superior to those in the left visual field (LVF)/RH, but no effect of semantic distance was observed. The SDT was performed equally quickly in both hemifields/hemispheres and a semantic distance effect was present with this task: RTs were faster to closely compared to distantly related category exemplars in both the RVF/LH and LVF/RH, and these effects were of equal magnitude in both hemifields/hemispheres. These findings suggest that hemispheric asymmetries in language processing in general and in semantic processing in particular are dynamic and adapt to task demands, and that the semantic processing capability of the RH is more likely to match that of the LH under explicit, but not implicit, processing conditions.

3.1.2. Introduction

The association between language deficits and LH lesions has been recognized since antiquity, yet only when John Hughlings Jackson proposed a RH advantage for visuospatial processing did the notion of a dichotomy in cognitive hemispheric capacities emerge (Jackson, 1874). This verbal-visuospatial dichotomy has evolved into a maxim in general neuropsychology, and it was against this backdrop that the first findings with callosotomy patients were published. It was thus not surprising that these patients could not name words visually presented to their left visual fields, but it was astonishing that their left hands could select the corresponding object from among an array (Gazzaniga & Sperry, 1967; Sperry, 1982). It appeared that hemispheric competencies for a given cognitive task were best modelled not as unilateral dichotomizations but as *relative* asymmetries. Among the most significant factors modulating these asymmetries are input/output modalities, or task demands.

Laterality research on language has thus concentrated on which aspects of language and under which conditions the RH demonstrates competency. The unique *semantic* capabilities of the LH and RH are commonly investigated in divided-visual field experiments with, paradoxically, *lexical* decision tasks (i.e. deciding whether a letter string is a real word). Two experimental approaches can be distinguished. Firstly, target stimulus words are *a priori* grouped into different semantic classes (e.g. concrete vs. abstract, high vs. low imageability) and the visual field/hemisphere with the superior performance for a given stimulus group is said to preferentially store or process this semantic information (Hines, 1976; Day, 1977; Jackman, 1985; McMullen & Bryden, 1987; Koenig, Wetzel & Caramazza, 1992). This approach is supported by numerous studies with non-lateralized stimulus presentations (James, 1975; Jastrzembski, 1981; Balota, 1994) demonstrating influences of the target word's semantic content on lexical

decision-making. For example, Chumbley and Balota (1984) performed a multiple regression analysis of several linguistic predictor variables (measures of word frequency and the number of dictionary meanings, word length, instance dominance and data from separate word association and pronunciation tasks) on the criterion variable of non-lateralized lexical decision RTs to determine which variables independently predicted performance. This analysis revealed significant predictive effects for the number of associates and associative RT, indicating that the semantic content of the target words independently contributed to lexical decision RT.

A second approach primes lexical decisions with words semantically related to the target word. These priming studies are generally based on the spreading activation theory of semantic processing, which postulates that once a concept is activated (e.g. by the presentation of a stimulus word), this activation automatically spreads through links in a semantic network to meaningful associates (Collins & Loftus, 1975). If activation spreads to a node representing the target word, the threshold for a response and RT of the lexical decision are reduced (Meyer & Schvaneveldt, 1971). Thus, if lexical decisions in a given hemifield are semantically primed, and thus facilitated, then the semantic relationship is presumably represented in the corresponding hemisphere (e.g. Chiarello, Senehi & Nuding, 1987; Chiarello, Burgess, Richards & Pollock, 1990; Abernethy & Coney, 1996). Divided-visual field priming experiments, however, have one major drawback: during the SOA the prime word becomes available to both hemispheres such that the opposite hemisphere can contribute or interfere with the lexical decision (Zaidel, White, Sakurai & Banks, 1988). Clearly, this confound is unavoidable for some research questions, such as the time course of semantic activation within the two hemispheres (Burgess & Simpson, 1988; Chiarello, Burgess, Richards & Pollock, 1990; Abernethy & Coney, 1993; Koivisto, 1997) or hemispheric

differences in controlled vs. automatic semantic processing (Chiarello, 1985; Koivisto & Laine, 2000; Koivisto & Hamalainen, 2002).

The approaches described above indirectly measure semantic processing in the two hemispheres; the explicit retrieval of semantic information is not required to perform the tasks. Although explicit retrieval is considered by some to be a defining characteristic of semantic memory (Warrington, 1975), it has been largely neglected in laterality research. The current study was designed to determine hemispheric patterns of semantic activation during implicit and explicit semantic processing. Two non-priming split-visual field paradigms were constructed, a unilateral lexical decision task (LDT) to assess implicit semantic processing and a unilateral semantic decision task (SDT; specifically, a category matching task, i.e. deciding whether two target words belong to the same category) to measure explicit semantic processing. The stimuli in the LDT consisted of word pairs representing exemplars from the same category and word-pseudoword foils. Identical target word pairs were employed in the SDT with foil exemplars from different categories. Since the target word pairs were identical in both tasks, performances in the two tasks differed only with respect to task instructions (demands). We planned to measure the possible presence and extent of semantic processing in each task by exploiting the known RT advantage for closely compared to distantly related categorical exemplars (semantic distance effect; Rips, Shoben & Smith, 1973; Caramazza, Hersh & Torgerson, 1976). Faster hemifield/hemispheric RTs with closely compared to distantly related category exemplars would indicate the appreciation of this semantic information. Target word pairs were thus *a priori* dichotomized along this dimension and presented once in a LDT to measure implicit and once in a SDT to measure explicit semantic processing (see Figure 11).

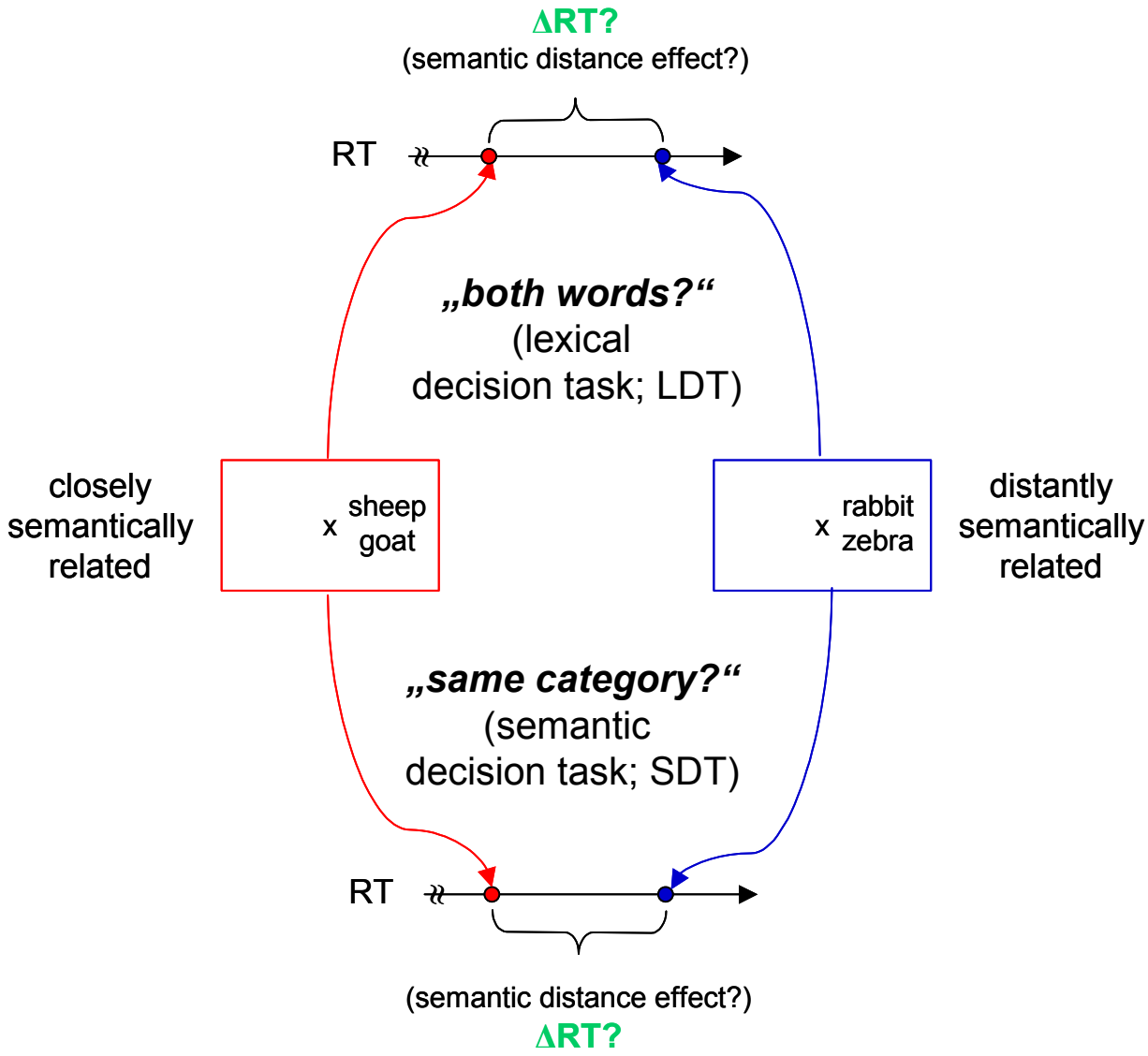


Figure 11. Experimental paradigms in Study 3.1.

3.1.3. Methods

3.1.3.1. Subjects

Twenty native Swiss-German-speaking, right-handed (mean Chapman and Chapman scale score ± SD = 13.5 ± 1.1; possible range 13.0 to 39.0, reflecting extreme right- and left-handedness, respectively; Chapman & Chapman, 1987; see Appendix A) men (mean age ± standard deviation (SD): 33.2 ± 7.6) participated in this experiment. No subject had a history of neurologic or psychiatric disease or of learning disabilities

according to a standardized interview adapted from Campbell (2000) and none had a specialized knowledge of linguistics.

3.1.3.2. Tachistoscopic tasks

Stimuli: Thirty-two pairs of words, each four to six letters in length, from four semantic categories (animals, fruits and vegetables, clothing and containers; 8 word pairs from each category) were selected such that half of the pairs from each semantic category were closely and half distantly semantically related. The written word frequencies (Baayen et al., 1995) of the closely vs. distantly related word pairs did not differ (the written word frequency for one word was not available; $t(61) = 1.50$, $p = 0.14$). An independent group of subjects (n = 17) rated the semantic distance of all pairs on a 6-point scale ("conceptually closely or distantly related?"). An unpaired *t*-test confirmed that the mean ratings of the closely and distantly related word pairs were significantly different ($t(30) = 15.59$; $p < .0001$; see Appendix B).

The LDT and SDT employed the same target ("go") stimuli. LDT "no-go" trials were constructed by pairing each "go" word with a pronounceable nonword and SDT "no-go" trials by pairing each "go" word with an exemplar from a completely different category. All stimuli were presented unilaterally and once for 120 msec in each visual field, resulting in 128 trials for each task. The pairs were presented in a fixed, pseudorandomized order such that consecutive trials did not contain more than three go or no-go pairs and such that the same stimulus pair did not appear consecutively in the two visual fields (see Figure 11).

Task: The letters of all stimuli were spaced such that the words extended from 1.2 to 4.0 degrees of visual angle from a central fixation cross. All stimuli were presented one

above the other unilaterally with a vertical distance of 0.8 degrees between them. Subjects were seated 57.5 cm from a computer screen measuring 28.2 cm in diameter with their chins resting on a chin rest. Subjects were instructed to fixate on a fixation cross presented in the center of the screen for 120 msec. 120 msec following the fixation stimulus, stimulus pairs were presented for 120 msec. Subjects responded with bilateral keypresses if both stimuli were words (LDT) or belonged to the same semantic category (SDT) and made no response otherwise. Subjects were informed of the semantic categories of the stimuli before the start of the lateralized SDT. Each task was preceded by 6 practice trials with different stimuli balanced for visual field followed by 128 experimental trials in 2 blocks of 64 presentations each. The order of task presentation was counterbalanced across subjects.

3.1.4. Results

3.1.4.1. Counterbalancing

RVF/LH and LVF/RH performance accuracies and the number of correct responses for the LDT and SDT are listed in the Table 1. Although performance accuracies in both hemifields and tasks were low, two-tailed *t*-tests revealed that these were significantly better than chance in both hemifields in both the LDT (both $p < .0001$) and SDT (both $p < .0001$). To determine whether the task order influenced performance, a repeated measures analysis of variance (ANOVA) was carried out with the factors counterbalancing condition (LDT –> SDT vs. SDT –> LDT) and task (LDT vs. SDT) as the within-subjects variables and accuracies in the LVF/RH and RVF/LH as the repeated measure. The main effect of counterbalancing condition was not significant ($F(1) = .48$; $p = .49$) but a trend for higher accuracy in the SDT compared to the LDT

was revealed ($F(1) = 3.87$; $p = 0.057$). The interaction of counterbalancing condition x task was significant ($F(1) = 4.72$; $p < .05$), indicating better performance on the second compared to the first task irrespective of which task was performed first (overall accuracies (%) ± SD: LDT presented first: 63.7 ± 7.4, presented last: 70.7 ± 9.6; SDT presented first: 70.2 ± 9.5, presented last: 73.8 ± 7.7). Although the main effect of visual field was significant ($F(1) = 31.51$; $p < .0001$), its interactions with task and task

Table 1. Accuracies and number of correct responses to all stimuli and to closely vs. distantly semantically related items in the unilateral lexical (LDT) and semantic decision (SDT) tasks in the RVF/LH and LVF/RH.

		Number Correct		
	Accuracy (%)	total	close	distant
LDT:				
RVF/LH	69.7 ± 10.0	21.9 ± 6.1	12.0 ± 3.3	9.9 ± 3.3
LVF/RH	64.8 ± 7.6	19.1 ± 5.4	10.9 ± 3.0	8.2 ± 3.0
SDT:				
RVF/LH	75.2 ± 9.6	22.3 ± 3.5	13.0 ± 2.4	9.3 ± 1.8
LVF/RH	68.8 ± 6.6	18.2 ± 4.6	11.2 ± 2.1	7.1 ± 2.9

order were not, indicating that *both* hemispheres benefited comparably from practice with a lateralized task. The data from both counterbalancing groups were therefore collapsed for further analyses.

3.1.4.2. General Performance on the LDT and SDT

A repeated measures ANOVA of the number of correct responses with visual field as the repeated measure and task (LDT vs. SDT) as the within-subjects factor

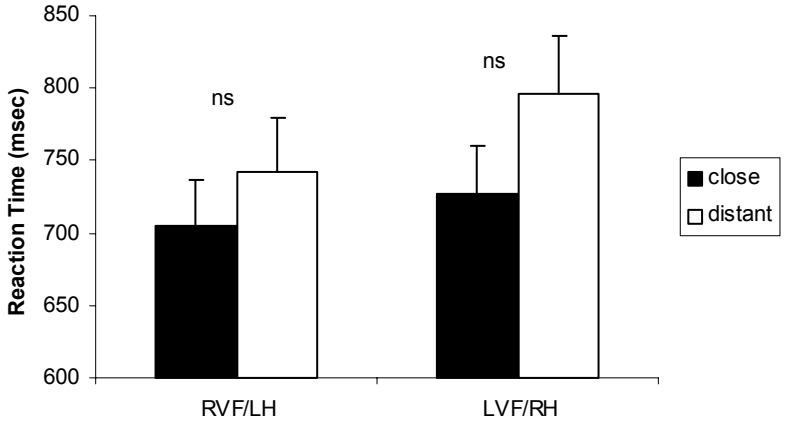
revealed a single significant effect of visual field ($F(1, 38) = 238.05$; $p = .0001$) reflecting the overall greater number of hits in the RVF/LH compared to the LVF/RH ($t(39) = 4.32$; $p = .0001$). The same ANOVA with RTs revealed main effects for both visual field ($F(1, 38) = 7.87$; $p < .01$; overall faster RVF/LH RTs; $t(39) = 2.82$; $p < .01$) and task ($F(1, 38) = 6.10$; $p < .05$; overall faster LDT RTs; $t(78) = 3.43$; $p = .001$), but no significant interaction. The presence and magnitude of semantic processing under implicit (LDT) and explicit (SDT) task demands were next tested by comparing RT differences to closely vs. distantly related target word pairs.

3.1.4.3. Testing for presence and extent of semantic processing in the LDT and SDT

A repeated measures ANOVA of RTs with visual field as the repeated measure and task (LDT and SDT) and semantic distance (closely vs. distantly related category exemplars) as within-subjects variables revealed the aforementioned main effects of visual field ($F(1, 76) = 9.03$; $p < .01$) and task ($F(1, 76) = 12.38$; $p < .001$) as well as a significant main effect of semantic distance ($F(1, 76) = 4.34$; $p < .05$; overall faster RTs for closely related stimuli; $t(158) = 2.64$; $p < .01$). All interactions were nonsignificant.

Hemispheric differences for semantic processing under the implicit and explicit semantic conditions were next investigated with separate repeated measures ANOVAs for the LDT and SDT. These uncovered task differences in the form of a double dissociation: the only significant effect in the LDT ANOVA was of visual field ($F(1, 38) = 6.89$, $p = .01$; but not of semantic distance ($F(1) = 1.19$, $p = .28$)), whereas the only significant effect in the SDT was of semantic distance ($F(1, 38) = 4.33$, $p < .05$; but not of visual field ($F(1) = 2.68$, $p = .11$)). The magnitudes of the semantic distance effects in the RVF/LH and LVF/RH in the SDT were equivalent ($t(19) = .26$; $p = .80$; see Figure 12).

a) LDT (implicit semantic processing)



b) SDT (explicit semantic processing)

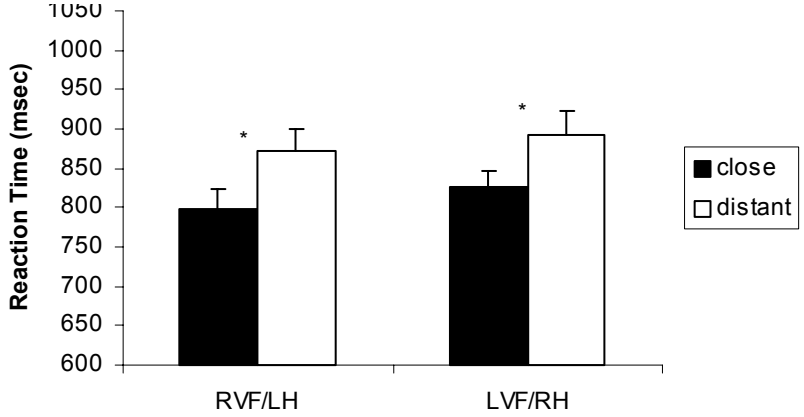


Figure 12. Mean (with standard errors) left visual field (LVF)/RH and right visual field (RVF)/LH reaction time (RT) performances to closely and distantly categorically related stimuli in the a) LDT (implicit semantic task) and b) SDT (explicit semantic task) of Study 3.1.

3.1.5. Discussion

Overall more correct responses and faster RTs were made in the RVF/LH compared to the LVF/RH, a finding consistent with the axiomatic LH dominance for language. Hemispheric performances, however, were significantly modified by task demands: the common RVF/LH advantage in terms of RTs was only evidenced in the LDT, whereas hemispheric RT performances on the SDT were equivalent. Thus, in terms of RTs to identical target stimuli, the RH performed more poorly than the LH when

asked a lexical question, but performed as well as the LH when asked a semantic question.

Explicit measures may direct attentional resources to the semantic fields containing the stimuli and thereby induce controlled, as opposed to automatic, semantic processing conditions. Thus, the present LDT may be conceived of as promoting automatic and the SDT controlled semantic processing. This distinction, however, may not be applicable to the current study for the following reasons. Firstly, although a large body of evidence supports automatic semantic processing in both hemispheres (Collins, 1999; Shibahara & Lucero-Wagoner, 2002) or just the LH (Koivisto, 1998; Koivisto, 1999; Koivisto & Laine, 2000), LDT performances in both hemispheres did not evidence the semantic distance effects telling of automatic semantic processing. On the other hand, several studies have suggested that the RH may be disadvantaged at controlled processing (Burgess & Simpson, 1988; Chiarello, 1988; Chiarello, Burgess, Richards & Pollock, 1990). The paradigmatic parameters which induce automatic processing lead only to facilitory effects whereas those inducing controlled processing lead to early, facilitory effects as well as late, inhibitory effects (Posner & Snyder, 1975). Since an immediate response was required by the present SDT, it is not possible to dissociate whether the facilitated responses arose from automatic or early controlled processing. It therefore appears more prudent to adopt the stance that the current LDT simply represented an implicit and the SDT an explicit semantic task. Such explicit measures may offer an alternative approach to the study of hemispheric semantics, in particular qualitative hemispheric differences in explicit semantic processing.

The extent of semantic processing under implicit and explicit processing conditions was assessed by taking advantage of known RT advantages for closely vs. distantly related categorical stimuli ("semantic distance effect"). That is, RT advantages

for closely vs. distantly related words indicate that these semantic relationships had been appreciated. No effect of semantic distance was observed under implicit semantic processing conditions (i.e. the LDT) in either hemisphere. When semantic processing was explicitly tested (i.e. in the SDT), however, significant effects of semantic distance emerged in both hemifields/hemispheres.

SDTs similar to the one employed here have previously been employed to investigate hemispheric differences in explicit semantic processing. For example, category membership decisions (i.e., deciding whether a laterally presented exemplar is a member of a foveally presented superordinate category) were made equally quickly in both hemifields/hemispheres (Day, 1977; Urcuioli, Klein & Day, 1981). Category matching decisions (i.e., deciding whether one foveally and one laterally presented exemplar belonged to the same superordinate category), on the other hand, have shown RVF/LH advantages in terms of RTs (Urcuioli, Klein & Day, 1981; see also Gross, 1972). In the present study, both stimulus words were unilaterally presented to rule out the participation of the opposite hemisphere, and comparable RT performances on this category matching task were observed in the two hemifields (see also Taylor, Brugger, Weniger & Regard, 1999). Moreover, both hemifields/hemispheres evidenced significant semantic distance effects, and these effects were equal in magnitude. The present findings thus extend previous ones by demonstrating equivalent explicit semantic processing capacities in the two hemispheres as measured by semantic distance effects. Overall, the hemispheric asymmetries adapted to meet the changing task demands, and both hemisphere's semantic answer depended on the question asked.

Study 3.2. Deconstructing an Axiom: A Shift to Right Hemisphere Language Dominance during pure Semantic Processing

3.2.1. Abstract

The assumption of a LH dominance for language processing has an axiomatic status within neurology. It has repeatedly been supported by functional imaging studies, which typically employed tasks that required both the retrieval of the word form (lexical analyses) and meaning (semantic analyses). This approach, however, neglects the clinical and experimental evidence that while the LH dominates lexical analyses, RH language competence primarily comes into play at the level of semantics. We designed three series of functional MRI tasks, each with a unique orthographic, lexical and semantic paradigm, to separately target lexical and semantic processing and to quantify the hemispheric competencies for each. Two regions were commonly activated during all lexical tasks: the left medial frontal lobe and the left angular and/or supramarginal gyrus. Semantic processing was consistently associated with bilateral inferior and superior frontal as well as right middle temporal, right medial frontal and right cingulate activity in the first two task series. Laterality indices indicated a LH dominance for all lexical tasks and a shift to RH processing during all semantic tasks. These findings demonstrate that the RH language system is significantly engaged at the level of meaning analysis in classic language tasks and provide a conceptual basis for its known ability to appreciate metaphors and unusual semantic relationships.

3.2.2. Introduction

The LH predominance for language is epitomized by the aphasic syndromes which result from LH lesions. Neuropsychological experimentation has revealed, however, that also RH brain damaged individuals exhibit distinct language impairments: in addition to their known inability to appreciate metaphors (Winner & Gardner, 1977), also instances of subtle semantic, i.e. conceptual, deficits have been documented: reduced semantic clustering in free recall portions of verbal learning tasks (Villardita, Grioli & Quattropani, 1988), poor categorization of familiar objects (Incisa della Rocchetta, 1986), an increased number of idiosyncratic or unrelated responses to single word associations (Glosser & Goodglass, 1991) and poorer semantic compared to phonemic fluency performance (Joanette & Goulet, 1988). Semantic competence has also been demonstrated in the disconnected RHs of callosotomy patients. Disconnected RHs not only understood written language, but also appreciate superordinate-subordinate and functionality relationships (Zaidel, 1978), matched printed synonyms and antonyms (Zaidel, 1982) and evidenced semantic priming effects for lexical decisions (i.e., deciding whether a letter string is a real word or not; Zaidel, 1983). Finally, it is implausible that a RH language capacity arises solely from potential functional reorganization initiated by disease or accident, as this ability has also been demonstrated in healthy RHs. While RVF/LH performances on split visual field tasks which present verbal stimuli separately to the RVF/LH and LVF/RH are typically superior to those in the LVF/RH on lexical tasks which require access to the word form lexicon for word identification (Chiarello & Beeman, 1998), hemispheric performances can match when the word meaning must be retrieved to solve a semantic task (Urcuioli, Klein & Day, 1981).

Although the functional neuroanatomical characterization of the RH conceptual system would have both weighty theoretical and clinical (i.e. neurorehabilitative) consequences, the anticipated contributions from functional imaging studies have not yet been forthcoming. Such studies using visual word stimuli have typically employed two types of subtraction methodologies to isolate semantic processing: the subtraction of activations during complex visual or during phonological baseline tasks from those during semantic target tasks. Semantic relative to complex visual processing has generally localized the former to the inferior frontal gyrus (Price, Wise et al., 1994; Pugh et al., 1996; Vandenberghe, Price, Wise, Josephs & Frackowiak, 1996; Beauregard et al., 1997; Rumsey et al., 1997), regions near or at the inferior parietal cortices (BA 39, 40; Howard et al., 1992; Rumsey et al., 1997; Hart, Kraut, Kremen, Soher & Gordon, 2000), different regions of the temporal cortex including the middle (Pugh et al., 1996; Vandenberghe, Price, Wise, Josephs & Frackowiak, 1996; Beauregard et al., 1997), medial (Price et al., 1994; Beauregard et al., 1997) and superior temporal gyri (Pugh et al., 1996; Vandenberghe, Price, Wise, Josephs & Frackowiak, 1996), the anterior cingulate gyrus (Beauregard et al., 1997; Rumsey et al., 1997) and the lingual and (Price et al., 1994)/ or fusiform (Beauregard et al., 1997; Rumsey et al., 1997) gyri. The subtraction of activations during phonological baseline tasks (employed to control for automatic phonological processing; Van Orden, Johnston & Hale, 1988) from those during semantic target tasks has resulted in similar activation patterns (Price, Moore, Humphreys & Wise, 1997; Rumsey et al., 1997; Mummery, Patterson, Hodges & Price, 1998; Moore & Price, 1999; Poldrack et al., 1999). Significantly, the regions found activated with both subtraction methodologies were either LH-dominant (Price et al., 1994; Pugh et al., 1996; Beauregard et al., 1997; Rumsey et al., 1997; Mummery, Patterson, Hodges & Price, 1998; Poldrack et al., 1999) or completely isolated to LH

cortical regions (Howard et al., 1992; Vandenberghe, Price, Wise, Josephs & Frackowiak, 1996; Price, Moore, Humphreys & Wise, 1997; Rumsey et al., 1997; for a review, see Binder & Price, 2000).

The surprisingly minimal or complete lack of RH cortical activation may be the consequence of subtraction procedures which extracted combined lexical *and* semantic processes and thus disadvantaged the lexically less competent RH. Furthermore, the singling out of isolated regions of interest presumes homotopic organizational principles, i.e. that functionally equivalent abilities are localized at mirror image sites in the two hemispheres. However, language functions in the RH may be more diffusely organized (Semmes, 1968; see also Fiez & Petersen, 1998), as suggested by clinical findings that deficits on basic speech act abilities following LH and RH lesions are correlated with LH but not RH lesions sites (Zaidel et al., 2000).

The current study was designed to isolate lexical and semantic components of written language processing and to quantify LH and RH contributions to each. Three series of functional MRI tasks were employed to assess the reliability of the results. Each was designed with a unique orthographic, lexical and semantic paradigm. We planned to target lexical processes by subtracting activations during orthographic from those during lexical tasks, and to target semantic processes by subtracting activations during lexical from those during semantic tasks.

3.2.3. Methods

3.2.3.1. Subjects

Nine healthy, right-handed (mean Chapman and Chapman score ± standard deviation (SD) = 13.4 ± 0.9; Chapman & Chapman, 1987; see Appendix A), native German-speaking men (mean age ± SD = 29.3 ± 5.8) participated in the study. No

participant had a history of neurological or psychiatric diseases according to a standardized interview adapted from Campbell (2000) or of learning disabilities. All signed informed consent and were compensated for their participation. The experimental protocol had been approved by the local hospital ethics committee.

3.2.3.2. Experimental Design

Three series of tasks were constructed to determine regions of task-independent sites of activation, each with a unique orthographic, lexical and semantic paradigm (see Table 2). Two types of activation subtractions were planned to target lexical (activations during lexical minus those during orthographic tasks) and semantic (activations during semantic minus those during lexical tasks) processing. Each task required GO/NOGO decisions to 45 pseudorandomly ordered stimuli of which circa 50% (i.e., either 12 or 13 stimuli) were GO stimuli.

Task series 1 consisted of a feature identification paradigm (orthographic task; closed letter in five-letter strings). The lexical task exploited the word superiority effect (Reicher, 1969), i.e. the ”top-down” facilitation from lexical processing when identifying a prespecified letter (‘T’) embedded in a real word (50% of trials) compared to consonant strings. The semantic task required subjects to judge the meaningfulness of words, i.e. whether a given word elicited relatively many associations (Paivio, Yuille & Madigan, 1968). Twenty-two words with high and twenty-three words with low meaningfulness were selected to significantly differ with respect to meaningfulness but not imageability ($t(43) = 6.38$, $p < .0001$ and $t(43) = 1.19$, $p = 0.24$, respectively; Hager & Hasselhorn, 1994).

Table 2. Experimental design and paradigms in functional imaging study.

		GO	NOGO
Task Series 1:			
SEM:	**meaningfulness**:	**meaningful**	**not meaningful**
	stimuli:	40 highly meaningful words	40 low meaningful words
LEX:	**letter identification**:	**letter "t"**	**no letter "t"**
	stimuli:	40 CS† w. "t"	40 CS without "t"
ORTH:	**feature detection**:	**closed letter**	**no closed letter**
	stimuli:	40 CS with closed letter	40 CS without closed letter
Task Series 2:			
SEM:	**imageability:**	**imageable**	**not imageable**
	stimuli:	40 high imageability words	40 low imageability words
LEX:	**pseudowords:**	**looks like word**	**doesn't look like word**
	stimuli:	40 pseudowords	40 CS
ORTH:	**scripted letters:**	**looks like German letter**	**does not look like G. letter**
	stimuli:	40 strings of Greek letters	40 strings of false fonts
Task Series 3:			
SEM:	**category membership:**	**fruit / vegetable**	**non-fruit / vegetable**
	stimuli:	40 fruits/vegetables	40 non fruits/vegetables
LEX:	**lexical decisions:**	**word**	**nonword**
	stimuli:	40 words	40 CS
ORTH:	**orthographic decisions:**	**German letter**	**non-German letter**
	stimuli:	40 CS	40 CS of Greek letters

† CS = consonant string

Task series 2's orthographic paradigm required subjects to identify a German letter in five-symbol strings of false fonts. In the lexical task, subjects judged whether German pseudowords and Finnish words (i.e., orthographically dissimilar to German) *looked like* real German words. In the semantic task, subjects responded when the word represented a tangible object, i.e., was highly imageable (Paivio, Yuille & Madigan, 1968). These words were selected such that 23 words were highly and 22 moderately imageable ($t(43) = 9.45$; $p < .0001$) while not differing with respect to meaningfulness ($t(43) = 1.26$, $p = .21$; Hager & Hasselhorn, 1994).

The orthographic task in series 3 presented subjects with 5-letter strings of either German or Greek letters and required subjects to respond when they recognised German letters. The lexical task was a lexical decision task with real German words and consonant strings and the semantic paradigm was a category decision task (i.e., GO fruits/vegetables; see Appendix C).

All subjects were administered the task series in the following order: series 1 – series 2 – series 3. Within each task series, each paradigm was presented three times, each time with one third of the stimuli, and in a counterbalanced order (i.e., ABCABCABC, BCABCABCA, CABCABCAB). For each subject, the particular counterbalancing condition remained constant over all task series. Each paradigm consisted of a total of 45 stimuli, which were presented for 1 sec with an interstimulus interval of 2 seconds. Bilateral keypresses were required for GO and no response for NOGO decisions. Behavioral data (accuracy and RTs) were analyzed with Kruskal Wallis and Mann-Whitney U tests. Due to technical difficulties, one subject could not be administered task series 1 and one subject task series 3.

3.2.3.3. Stimulus Presentation

The visual stimulus material was presented to the subjects with a computer-driven video back projection system synchronized to fMRI acquisition. Subjects viewed the stimuli via a mirror attached to the head coil. Subjects' responses in the magnet were recorded by an MR-compatible, optically linked response pad (FORP, Current Designs Inc., Philadelphia, PA).

3.2.3.4. Imaging procedures

Anatomical and functional MRI data were collected on a commercial 1.5 Tesla scanner (Signa Horizon NV; General Electric Medical Systems, Milwaukee, WI) with a standard head coil. Head motion was restricted by restraining straps and foam padding within the coil. Functional imaging was achieved with blood oxygenation level-dependent (BOLD) acquisitions. Thirty contiguous slices covering the entire brain (slice thickness 5 mm, nominal in-plane resolution of 2.5 x 2.5 mm) were acquired every three seconds using T2*-weighted, gradient-echo, single-shot, echo planar imaging (EPI) (i.e., TR = 3000 ms, TE = 40 ms, α = 70°, 1 excitation, rectangular FOV = 320 mm x 240 mm, imaging matrix = 128 x 96). Series of 80 sequential volumes were acquired for each functional experiment. Image acquisition was synchronized to the visual stimulus presentation (1 stimulus / 3 s). T1-weighted whole-brain anatomical reference volume data with an isotropic nominal spatial resolution of 1.2 mm were acquired at the beginning of each imaging session (TR = 50 ms, TE = 8 ms).

3.2.3.5. fMRI data analysis

All data post-processing and analyses were performed offline. To minimize artifacts due to residual head motion, functional volumes were realigned for each experiment using an automated image registration algorithm (Woods, Grafton, Watson, Sicotte & Mazziota, 1998). Subsequently, data were spatially filtered using a 3D Gaussian convolution kernel of 6mm at full-width half-maximum. Using a fully automated procedure, anatomical reference volumes were co-registered to the Montreal average volumetric data set aligned on the Talairach stereotactic coordinate system (Collins, Neelin, Peters & Evans, 1994). The resulting transformation was then used to resample all corresponding functional data sets into stereotactic space. The statistical

analysis of the functional series was carried out with a method based on a linear model with correlated errors (Worsley, Poline, Friston & Evans, 1997). The design matrix of the linear model was first convolved with a gamma variate hemodynamic response function. In a second step, experiments across subjects were combined using a random effect analysis also based on a linear model and contrasts resulting from the various subtractions of conditions were computed (Friston, Holmes, Price, Büchel & Worsley, 1999). The resulting T statistics images were thresholded at a significance level of $p < 0.05$ using the minimum given by a combination of Bonferroni correction and random field theory (Worsley, Marrett et al., 1996). The resulting group activation clusters are depicted superimposed on one subjects' anatomical image which had been transformed into stereotactic space and observed geometrical centers-of-gravity of clusters are reported in terms of the stereotactic coordinates of Talairach and Tournoux (1988). Furthermore, significant group activations from each lexical and semantic subtraction and from each task series were categorized and tabulated according to comprehensive, neuroanatomically defined regions of interest in the LH and RH (see Tables 3 and 4).

3.2.4. Results

3.2.4.1. Behavioral Results

The behavioral performances (mean accuracies and RTs) for all tasks are summarized in Table 3. All tasks which required objective judgments (all orthographic tasks, the lexical tasks in series 1 and 3, and the semantic task in series 3) were performed with above-chance accuracies (all $Z \geq 1.96$). The lexical task of series 1 was performed more accurately than the orthographic task ($U = 8.00$; $p < .01$). The RTs for all tasks in series 1 differed significantly ($H(2) = 18.35$; $p = .0001$); the lexical task

appeared easier than both the orthographic (U = 4.00; p < .01) and semantic (U = 0) tasks. Within the lexical task, letter identification was slower and more variable in letter strings compared to real words (RT ± SD = 596.10 ± 50.02 and 580.00 ± 38.87, respectively), as expected from the word superiority effect, but this difference did not reach statistical significance (t(20) = .87, p > .05). One reason for this negative finding is that both speed *and* accuracy were stressed to the subjects. The mean RTs in all tasks of series 2 were comparable (H(2) = 3.64; p = .16). The performance measures in series three differed over all tasks (accuracies: H(2) = 10.22, p < .01; RTs: H(2) = 8.84, p < .05). Analyses revealed that the semantic task was performed less accurately and more slowly than both the orthographic (U = 8.50, p < .05 and U = 7.00, p < .01, respectively) and lexical (U = 7.00, p < .01 and U = 10.00, p < .05, respectively) tasks, whose accuracies and RTs did not differ (both U > 15).

Table 3. Mean % Accuracy and RTs (msec) (+/- standard deviations) of the orthographic, lexical and semantic tasks in each task series (n=9) of Study 3.2.

	Orthographic	Lexical	Semanticoverall (Kruskal Wallis Test)		O-L	L-S	O-S
Task Series 1							
Accuracy (%)	82.8 ± 19.3	98.1 ± 3.2	n/a	n/a	U = 4 **	n/a	n/a
RT (msec)	710.8 ± 70.2	575.1 ± 55.1	793.6 ± 60.9	H(df=2) = 18.4 ***	U = 4 **	U = 0 ***	U = 15 *
Task Series 2							
Accuracy (%)	68.1 ± 14.1	n/a	n/a	n/a	n/a	n/a	n/a
RT (msec)	737.2 ± 64.5	776.7 ± 66.7	708.5 ± 60.2	H(df=2) = 3.6 (ns)	-	-	-
Task Series 3							
Accuracy (%)	93.8 ±8.7	95.6 ± 10.7	75.0 ± 24.3	H(df=2) = 10.2 **	U = 16 (ns)	U = 7 **	U = 8.5 *
RT (msec)	559.4 ± 94.1	599.8 ±86.6	717.2 ±59.7	H(df=2) = 8.8 *	U = 23 (ns)	U = 7 **	U = 10 *

* = p < .05; ** = p < .01; *** = p = .001

3.2.4.2. fMRI Results

3.2.4.2.1. Lexical subtractions

The strongest and largest activation associated with lexical processing in task series 1 was centered in the left angular gyrus. Weaker and smaller right inferior parietal lobe activations were also found and included the supramarginal and angular gyri. Left middle (BA 21) and right superior (BA 38) temporal activity was apparent. Finally, bilateral medial, left middle and right superior frontal lobe and left cingulate (BA 31) activations were also noted.

The lexical subtraction in task series 2 resulted in a widespread, left-lateralized network of activations with four distinct clusters in the left inferior parietal lobe including the supramarginal gyrus. Additional sites of parietal activations included the left superior parietal lobe (BA 7) and postcentral gyrus. Left medial (BA 34) and left-lateralized middle (BA 21) temporal activations were noted, as well as right inferior (BA 20) and superior (BA 22) temporal gyral activation. Widespread areas of the frontal lobes were activated in this subtraction, most extensively in the bilateral inferior frontal lobes (BA 45, 47). Left cingulate (BA 32), caudate nucleus and right-lateralized cerebellar activity were also found.

Task series 3's lexical subtraction revealed only one activated region in the left inferior parietal lobe: the supramarginal gyrus. Additionally, left inferior (BA 44, 46), medial (BA 11) and superior (BA 9, 11) frontal lobe and right cerebellar activations were found.

The brain regions significantly activated in each of the lexical subtractions are depicted according to regions of interest in Table 4. Two regions were consistently activated in all three lexical tasks: the left medial frontal lobe, commonly associated with

attentional processes, and the left inferior parietal lobe, specifically, the angular and/or supramarginal gyri (see Figure 13).

Table 4. Distinct (light gray) and Common (dark gray) Activations during isolated Lexical Processing in Study 3.2.

	Left Hemisphere			Right Hemisphere		
	Series 1	Series 2	Series 3	Series 1	Series 2	Series 3
Superior FL						
Middle FL						
Inferior FL						
Medial FL						
Superior TL						
MiddleTL						
Inferior TL						
Medial TL						
Superior PL						
Inferior PL						
Cingulate						
Caudate Nucleus						
Cerebellum						

FL = frontal lobe; TL = temporal lobe; PL = parietal lobe.

3.2.4.2.2. Semantic subtractions

The semantic subtraction in task series 1 revealed bilateral networks of activation in primarily temporo-frontal sites. Bilateral inferior (BA 20, L BA 17) and middle (BA 21) temporal activations were found in addition to right superior temporal (BA 38) activations. Inferior frontal (bilateral BA 47, left BA 45, and right BA 44) activations were also prominent among widespread activations primarily in middle and superior frontal sites (BA 6, 8, 9, 10, 46) as well as right medial frontal activations (BA 8, 10). Finally, left superior parietal (BA 7), right-lateralized cerebellar, right thalamic, right cingulate (BA 23, 24, 29) and right occipital (BA 19) activities were documented.

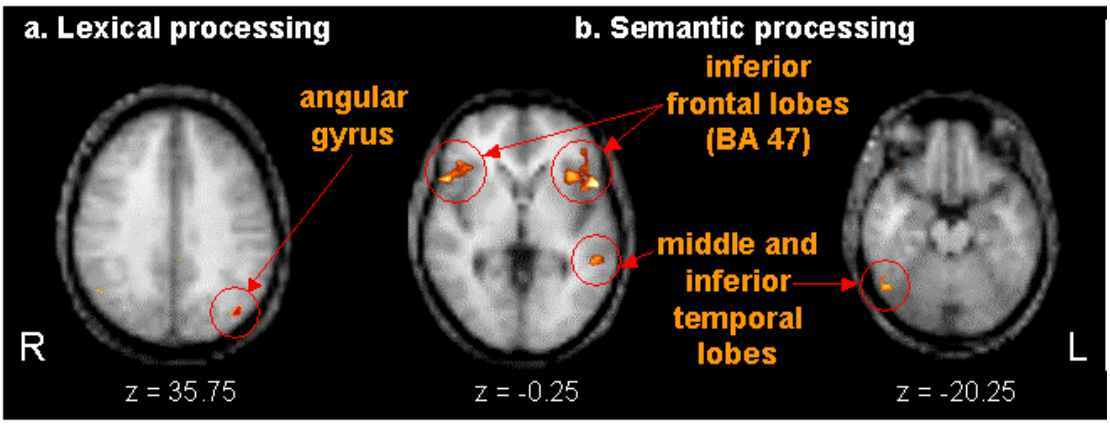


Figure 13. Sites of functional activation during isolated a) lexical and b) semantic processing. The left angular gyrus was significantly activated during lexical (compared to orthographic) processing in task series 1 (a). The activation patterns during semantic (compared to lexical) processing in the same task series were, however, bilaterally distributed in the inferior frontal (centered in BA 47) and temporal lobes (left middle and right inferior temporal activations (b).

The only site of temporal lobe activation in the semantic subtraction in task series 2 was in the right middle temporal lobe (BA 21). Parietal lobe activations were also found in the right inferior parietal lobe (BA 39) and in the left cuneus (BA 19). Frontal lobe sites were activated bilaterally in inferior (BA 47), superior (BA 6, 10) and medial (right BA 10, medially in the left gyrus rectus, BA 11) frontal lobes. RH cingulate activity was also apparent (BA 23, 31, 32).

The semantic subtraction in task series 3 failed to reveal significantly activated clusters in the temporal lobes. Instead, activations were largely restricted to bilateral frontal lobe sites, including inferior (BA 44/45, 47), middle (BA 9, 11) and superior (BA 8, 9) gyri. An isolated region left cingulate (BA 24) activity was also detected. Left temporal lobe activation commonly associated with semantic processing (Pugh et al., 1996; Vandenberghe, Price, Wise, Josephs & Frackowiak, 1996; Beauregard et al., 1997) was not apparent in the semantic subtraction of task series 3, perhaps because this task series was always administered last. Consequently, these regions may have become hyperperfused and subtle changes in activity related to semantic processing minimized, akin to described practice and repetition effects (Raichle, Fiez et al., 1994;

Garavan, Kelley, Rosen, Rao & Stein, 2000). Additionally, our subjects may have become fatigued by the end of the long experiment, thus reducing attentional capacity and hemodynamic responses (Jäncke, Mirzazade & Shah, 1999), an explanation supported by the lack of cingulate and medial frontal activation in this semantic subtraction.

Areas significantly activated during each of the semantic subtractions are listed according to region of interest in Table 5. Bilateral inferior frontal and right superior frontal sites were consistently activated in all three semantic subtractions. When only the first two task series were considered, the areas additionally consistently activated included the superior frontal lobe of the LH as well as the right middle temporal and medial frontal lobes and the right cingulate gyrus (see Table 5 and Figure 13).

Table 5. Distinct (light gray) and Common (dark gray) Activations during isolated Semantic Processing.

	Left Hemisphere				Right Hemisphere		
	Series 1	Series 2	Series 3		Series 1	Series 2	Series 3
Superior FL							
Middle FL							
Inferior FL							
Medial FL							
Superior TL							
Middle TL							
Inferior TL							
Medial TL							
Superior PL							
Inferior PL							
Cingulate							
Caudate Nucleus							
Cerebellum							

FL = frontal lobe; TL = temporal lobe; PL = parietal lobe.

3.2.4.2.3. Laterality Indices

Functional laterality for lexical and semantic processing was quantified with laterality indices for each task subtraction ((number of significantly activated RH voxels (RHV) – number of significantly activated LH voxels (LHV)) / (RHV+LHV); where positive values indicate a RH and negative values a LH functional superiority). As depicted in Table 6, all lexical subtractions yielded a LH and two semantic subtractions a RH functional superiority. Significantly, functional dominance during 1) lexical and 2) semantic processing (ΔLI) shifted towards the RH in all task series.

Table 6. Functional Hemispheric Dominance during Lexical and Semantic Processing.

	Lexical Processing			Semantic Processing			ΔLI
	LH	RH	LI	LH	RH	LI	
Task Series 1:	78	14	- 0.696	184	305	+ 0.247	+ 0.943
Task Series 2:	266	169	- 0.223	11	11	0	+ 0.223
Task Series 3:	11	2	- 0.692	23	26	+ 0.061	+ 0.753

3.2.5. Discussion

The present study documented a LH functional superiority for lexical (word-form) processing, as expected. During isolated semantic processing of the written language stimuli, however, functional activity in the RH predominated. Since LH sites associated with semantic processing (middle temporal and inferior frontal lobes; Binder & Price, 2000) were already activated during the lexical tasks, the present findings reflect an increase in RH, but not LH, activity as task demands changed from lexical to semantic. These findings clearly support a RH semantic competence for written, as opposed to auditory (Zahn, Huber et al., 2000), language material.

The ability of the RH to appreciate atypical or unusual semantic relationships has long been recognized. Metaphor comprehension, for instance, requires the nonliteral reading of literally unrelated material and is uniquely associated with the intact RH (Winner & Gardner, 1977; Brownell, 1988; see also Bottini, Corcoran et al., 1994; Kircher, Brammer, Andreu, WIlliams & McGuire, 2001). Recently, the generation of atypical or unusual verbs in response to noun targets was found to activate right frontal regions (Seger, Desmond, Glover & Gabrieli, 2000), and an event-related fMRI study reported significant increases in right inferior and middle frontal activity during the implicit processing of semantically anomalous verb-noun phrases (Min Kang, Constable, Gore & Avrutin, 1999). Moreover, several studies have documented right middle and superior temporal activations while subjects processed sentences with semantic violations (e.g., Kuperberg, McGuire et al., 2000). Clearly, a semantic system must exist to support this type of language ability.

The patterns of activation found with the lexical and semantic subtractions correspond to those found with similar paradigms and thus lend further support to the quantitative analyses. Isolated lexical processing was consistently associated with activation in the left medial frontal lobe, thought to reflect attentional processes, and the left inferior parietal lobe, i.e. the angular and/or supramarginal gyri. The angular gyrus of the inferior parietal lobe corresponds to Déjérine's site of visual word images (Déjérine, 1892), a structure which according to the classical neurological model of language processing is essential in processing word forms and mapping these onto linguistic representations (Geschwind, 1965; Benson & Geschwind, 1969). Indeed, damage to the left angular gyrus itself presumably results in the loss of the visual word images necessary for both reading and writing (alexia with agraphia), while its disconnection from occipital sites is thought to underlie pure alexia. This relationship is generally

confirmed by the present as well as other functional imaging studies which reported significant left angular as well as supramarginal gyral activations during lexicosemantic compared to complex visual processing tasks (Howard et al., 1992; Rumsey et al., 1997; Hart, Kraut, Kremen, Soher & Gordon, 2000). The language-related functions of the left angular and supramarginal gyri have been extended by functional imaging studies which documented activations during auditory lexicosemantic processing (e.g., semantic compared to phonetic monitoring; Démonet, Chollet et al., 1992), during phonological processing of written words (e.g., syllable counting compared to living/nonliving judgments; Price, Moore, Humphreys & Wise, 1997) and during generation tasks (e.g., verb generation compared to a verb-noun comparison task; Warburton, Wise et al., 1996). The left inferior parietal lobe may thus represent a region essential for multimodal, as opposed to purely visual, lexical processing.

Recent functional imaging studies have highlighted the contribution of the inferior temporo-occipital cortex in orthographic, lexical and semantic processing (Büchel, Price & Friston, 1998; Moore & Price, 1999; Cohen, Dehaene et al., 2000; see also Nobre, Allison & McCarthy, 1994). The participation of this region in specifically word form recognition is supported by isolated reports of pure alexia following left inferior temporo-occipital lesions (e.g., Henderson, Alexander & Naeser, 1985) and the left inferior temporo-occipital region is currently viewed as representing one critical node in a network for written word identification which includes the inferior parietal lobe (Henderson, 1986; Wise, Howard et al., 2000). Consistent left inferior temporo-occipital activations were not revealed by the lexical subtractions, although the block design of the present experiment may have masked early activity in this region (see e.g., Cohen et al., 2000).

Semantic processing was related to bilateral inferior frontal and right superior frontal activation in all three task series. The bilateral inferior frontal lobe activity presumably reflects both semantic selection (Thompson-Schill, D'Esposito, Aguirre & Farah, 1997) and phonological processes (Price, Indefrey & van Turennout, 1999): although semantic, and not phonological, decisions were explicitly required and although a direct, lexical-to-semantic reading route is preferred when reading for comprehension (Coltheart, 1987), semantic decision-making nevertheless elicits parallel phonological processing (Van Orden, Jansen op de Haar & Bosman, 1997). Superior frontal activation has also been reported during semantic tasks (Vandenberghe, Price, Wise, Josephs & Frackowiak, 1996; Mummery, Patterson, Hodges & Price, 1998), yet lesions here do not result in semantic deficits. Instead, these regions with their bi-directional temporal lobe connections and cingulate gyrus efferents may have been involved in attentional processes and/or the executive function of performance monitoring (Mummery, Patterson, Hodges & Price, 1998; Carter, Botvinick & Cohen, 1999). When the conjunction analysis was restricted to the first two task series, consistent middle temporal lobe activity related to semantic processing (Binder & Price, 2000) was apparent only in the RH.

The semantic subtraction of task series one (meaningfulness decision vs. letter identification) resulted in many more regions of significant activation compared to the semantic subtraction of task series two (imagery vs. visual word decision): bilateral middle frontal lobe and inferior temporal lobe, the left middle and right superior temporal lobe and the left superior parietal lobe. One reason for the more extensive activations in the first semantic subtraction is the low-level nature of its baseline letter identification task compared to the higher-level lexical and phonological demands the baseline task in the second semantic subtraction. Moreover, the baseline task in the second semantic

subtraction employed pseudowords known to activate regions involved in semantic processing (inferior and middle temporal lobe; Price, Wise & Frackowiak, 1996); the employed subtraction procedure may have decreased the significance of activations in the same sites for the target task. Of particular interest, however, is the bilateral inferior temporal activations in the first compared to the second semantic subtraction. This significant activation in this region commonly associated semantic processing (Binder & Price, 2000) suggests that meaningfulness decisions more strongly tax the conceptual system than imagery decisions. An imagery decision, on the other hand, clearly requires visual semantic processes. Although the neuroanatomical differentiation of visual and non-visual semantic system has been questioned (Martin-Loeches, Hinojosa, Fernandez-Frias & Rubia, 2001), a recent fMRI study found occipito-parietal activation during visual imagery of acoustically presented animal names compared to the passive listening to abstract words (Lambert, Sampaio, Scheiber & Mauss, 2002). This finding is consistent with the present observation of right inferior parietal activation in the second (imageability decision) compared to the first (meaningfulness decision) semantic subtraction.

The anterior cingulate gyrus and related medial frontal lobe are known to support to language processing either with performance evaluation or motivated attention, selection for action, or conflict monitoring (see Carter, Botvinick & Cohen, 1999, for a review). Interestingly, the present primarily anterior cingulate activity was predominantly lateralized to the LH during lexical and RH during semantic processing, suggesting a flexible lateralization of the attentional or executive function network to the hemisphere with the greatest processing demands.

The present study demonstrates the existence of a RH conceptual system which significantly contributes to the appreciation of also common semantic relations. This

system may be overlooked by region of interest approaches which presume homotopic organizational principles. Indeed, clinical evidence suggests that comparable functional deficits are caused by lesions greater in size in the RH compared to the LH (Semmes, 1968; Zaidel et al., 2000). These findings indicate a more modularized functional organization in the LH compared to the RH, a hypothesis supported by hemispheric differences in microcircuitry revealed with neuronal tract tracing (Galuske, Schlote, Bratzke & Singer, 2000). A diffuse organization of functions in the RH is not only evolutionary meaningful, but functionally compatible with a broad activation of the semantic network (Beeman et al., 1994) particularly conducive to certain conceptual tasks (e.g., metaphor appreciation; Winner & Gardner, 1977). Clinically, the present findings suggest that lexical and phonological rather than semantic tasks should be employed to determine clinical language dominance. They also offer a focus for neurorehabilitation programs for aphasia, i.e. semantic language functions which have axiomatically, but perhaps too hastily, been considered the exclusive domain of the "language dominant" LH.

Study 3.3. Qualitative Hemispheric Differences in Semantic Category Matching

3.3.1. Abstract

A unilateral category matching task with words as stimuli was employed to investigate semantic processing in the RH and LH. An overall right visual field (RVF)/LH dominance was observed and performances were better than chance, also in the left visual field (LVF)/RH. A qualitative analysis of RTs with individual differences multidimensional scaling (INDSCAL) revealed that LVF/RH INDSCAL solutions were significantly more differentiated in structure than RVF/LH solutions in terms of number and size of dimensions. These findings support a “depth of activation” hypothesis of hemispheric processing, with the LH rapidly and focally and the RH slowly and diffusely activating the semantic network.

3.3.2. Introduction

Studies with split-brain patients provided an impetus for investigating the semantic language capabilities of the RH. Zaidel and his colleagues, for example, demonstrated that the disconnected RH is able to match printed synonyms and antonyms (Zaidel, 1982) and appreciate superordinate and subordinate relationships as well as functionality (Zaidel, 1978). Moreover, lexical decisions following semantically related primes were also facilitated in the RH (Zaidel, 1983). The picture that emerged depicted a RH that displayed a certain competence for semantic processing although the LH was superior on most language tasks. This view, however, has not gone unchallenged (e.g., Gazzaniga, 1983).

Zaidel's findings have nevertheless been supported by studies from brain-damaged populations. RH brain-damaged individuals have difficulties in appreciating connotative and metaphoric meanings or in drawing inferences (Wapner, Hamby & Gardner, 1981; Brownell, Potter & Michelow, 1984; Brownell, Simpson, Bihrle, Potter & Gardner, 1990). Furthermore, they exhibit a semantic clustering deficit for concrete but not abstract words in free recall portions of memory tasks (Villardita, Grioli & Quattropani, 1988) and have been found to perform worse on semantic fluency tasks compared to phonetic fluency tasks (Joanette & Goulet, 1988, but see Cardebat, Demonet et al., 1996). The convergence of results from these and other studies have supported the hypothesis that the RH has the potential for language processing at the lexicosemantic level (Joanette & Goulet, 1988).

A number of difficulties impede the direct generalizability of these findings to the healthy and connected RH. Not only do split-brain patients possess a transected corpus callosum, but they may also exhibit additional brain pathology induced by early epileptogenic lesions or by post-surgical compensations. Furthermore, it is unclear whether the pattern of performance in brain-damaged individuals is a result of plasticity of function in the impaired hemisphere or functional compensation or pathological inhibition from the opposite hemisphere (Zaidel, 1983). Thus, tachistoscopic studies with healthy individuals have been an important component in elucidating the limits of RH semantic linguistic capabilities.

Day (1977) investigated RH semantic competence with tachistoscopic tasks in healthy individuals. He found that category membership decisions (i.e., deciding whether a laterally presented word denoting a category exemplar is a member of a foveally presented superordinate category) were made equally fast in both the LVF and

RVF for concrete exemplars. Day suggested that both hemispheres were capable of recognizing and categorizing words representing common concrete objects.

These results were verified and extended by Urcuioli, Klein and Day (1981) with two categorization tasks: a category membership task identical in design to Day's (1977; Exp. 3) and a category matching task (i.e., deciding whether one foveally and one laterally presented exemplar belonged to the same superordinate category). The results of their semantic membership task supported Day's (1977) findings, namely comparable LVF and RVF performance with concrete exemplars. Category matching decisions, on the other hand, were faster in the RVF. This latter finding had also been reported by Gross (1972) using a unilateral category matching paradigm with ten subjects. Urcuioli et al. postulated that semantic membership decisions require the determination of the exemplar's superordinate category and then matching this superordinate category to that presented. Category matching decisions, on the other hand, require two superordinate determinations followed by a comparison of the categories. The authors argued that RH semantic competence broke down at the level of category matching because only the LH could perform simultaneous categorical decisions.

The studies outlined above seem to indicate that RH semantic competence ceases at the level of category matching decisions. Two notable issues, however, complicate this interpretation. First, because one of the target words in Urcuioli et al.'s (1981) category matching tasks was always presented foveally, the possible contributions or interferences of the opposite hemisphere cannot be ruled out (Zaidel, White, Sakurai & Banks, 1988). Secondly, assuming that the RTs in these experiments reflect the processing of a single hemisphere, slower RTs to stimuli presented to the LVF/RH relative to the RVF/LH may not necessarily imply the absence of RH

competence for this task. Indeed, analyses of accuracy (based on percent errors) in Urcuioli et al.'s (1981) and Gross's (1972) category matching experiments revealed no significant differences between visual fields. One alternative explanation of these findings is that the two hemispheres employ qualitatively different processing mechanisms in solving this task. Priming studies have offered two such processing hypotheses: the depth of activation hypothesis and the time-course hypothesis of hemispheric semantic processing.

Both hypotheses of hemispheric semantic processing focus on the automatic spread of activation between semantic features in a network. When a concept is activated, this activation spreads to semantically related items in the network. Decisions to semantically related word pairs or to targets preceded by a semantically related item will benefit from an overlap of activation and the responses will be facilitated (Collins & Loftus, 1975). Non-tachistoscopic category matching studies have thus obtained faster RTs for word pairs that were independently judged as more strongly semantically related than for word pairs that were judged as not semantically related (Rips, Shoben & Smith, 1973; Caramazza, Hersh & Torgerson, 1976). With respect to hemispheric processing, however, priming studies have found different patterns of facilitation in the RH and LH. These patterns differ in terms of when and how the semantic network is activated.

The depth of activation hypothesis postulates that the LH rapidly and focally activates the semantic network whereas RH activation is slow and diffuse. For example, Chiarello, Burgess, Richards and Pollock (1990) employed three kinds of semantic relationships in their priming experiment: semantically associated (Bee-Honey); semantically similar, defined as belonging to the same semantic category (Deer-Pony); and, semantically similar and associated (Doctor-Nurse). Subjects were either asked to

make lexical decisions or to name the targets. They found that no facilitation occurred in either visual field with associated primes, semantically similar primes facilitated responses only in the LVF/RH, and semantically similar and associated primes led to facilitated responses in both visual fields. These results did not vary as a function of task (lexical decision or naming; Chiarello, Burgess, Richards & Pollock, 1990).

Chiarello et al. (1990) explained these results in terms of the depth of activation hypothesis of hemispheric semantic processing. Pure similarity and similarity plus association priming occurred in the LVF because the RH was able to benefit from an overlap of spreading activation. Semantically similar primes did not lead to facilitated recognition of targets in the RVF, on the other hand, because the LH network was supposedly rapidly and focally activated. Priming in the RVF/LH was only evidenced when a large amount of semantic featural overlap existed between prime and target, as in the semantically similar plus associated condition. Because Chiarello et al. assume that associative priming takes place between the lexical forms of the stimuli, it is not surprising that no *semantic* facilitation occurred in either visual field in this condition.

Alternatively, the time-course hypothesis of semantic processing (Burgess & Simpson, 1988; Richards & Chiarello, 1995) postulates that both closely and distantly semantically related information are initially available to both hemispheres. Hemispheric differences only occur later in the time course of semantic activation when distantly related information becomes suppressed in the LH. This time course of activation is determined by the absence or presence of facilitation at differing SOAs, with initial processing supposedly being measured at SOAs of about 165 msec and late processing at SOAs of about 750 msec (Koivisto, 1997). Recent studies, however, have failed to find RH priming at short SOAs (e.g., Abernethy & Coney, 1996, with SOAs of 250 msec and 450 msec; Koivisto, 1997, with an SOA of 165 msec),

suggesting that the spread of semantic activation in the RH has a slower onset than that in the LH.

The current study was designed to further explore the limits of RH semantic processing ability with a tachistoscopic category matching task. To ensure the least amount of interhemispheric interference, a unilateral presentation was employed. If the results reported by Gross (1972) and Urcuioli et al. (1981) are attributable to the inability of the RH in making such decisions, then category matching decisions made in the LVF should not be different from chance. Furthermore, we planned to qualitatively analyze RTs in each visual field to investigate the influence of processing mechanisms on performance. Non-tachistoscopic category matching studies indicate that RTs on this task can be used to qualitatively investigate semantic processing; faster RTs were found with semantically similar word pairs than with semantically less similar word pairs (Rips, Shoben & Smith, 1973; Caramazza, Hersh & Torgerson, 1976). If performance on the category matching task is influenced by a depth of activation processing style, with the RH spreading its activation in a diffuse manner and the LH in a focal manner (Chiarello, Burgess, Richards & Pollock, 1990), then only LVF/RH category matching decisions will be able to benefit from an overlap of activation. This overlap will be manifested in consistently faster RTs to some stimuli compared with others. If performance is dictated by the time-course hypothesis of hemispheric processing, then RTs to category matching decisions made in both visual fields or the RVF/LH alone will evidence systematic differences.

3.3.3. Methods

3.3.3.1. Subjects

Twenty healthy (Campbell, 2000) men (ages 22 to 40, mean age 32.15 ± 5.37) participated in this experiment. All subjects were right-handed (Chapman & Chapman, 1987; see Appendix A) and native German speakers and none of the subjects had previously participated in a tachistoscopic experiment.

3.3.3.2. Experimental Design

3.3.3.2.1. Stimuli

The stimuli were ten 4- to 7-letter German animal names matched in length and frequency of production in a category association task (Mannhaupt, 1983) to 10 bird names. A Mann-Whitney U test revealed no significant difference between the production norms of the animal and bird names ($U = 33.50$; $p = 0.21$). The “go” stimuli represented every possible combination of two animals and two birds (45 x 2 = 90 pairs), and the “no-go” stimuli were an equal number of animal-bird pairs selected such that every word was presented an additional nine times. All stimuli were presented once to the LVF and once to the RVF, resulting in 360 presentations (90 x 2 x 2). The pairs were presented in a fixed, pseudorandomized order such that no stimulus item appeared more than three consecutive times and the same pair did not consecutively appear in the two visual fields (see Appendix D).

3.3.3.2.2. Task

The letters of all stimuli were spaced such that all extended from 1.2 to 4.0 degrees of visual angle. All stimuli were presented one above the other unilaterally with a vertical distance of 0.8 degrees between them. Subjects were seated 57.5 cm from a

computer screen measuring 28.2 cm in diameter. Subjects were instructed to fixate on a fixation cross presented in the center of the screen for 120 msec. 120 msec following the fixation stimulus, stimulus pairs were presented for 150 msec. Subjects were instructed to respond as quickly as possible by simultaneously pressing two keys with both the right and left index fingers if the two stimuli belonged to the same category, and to make no response if the stimuli belonged to different categories. Subjects were informed of the categories before the start of the experiment. Because a large number of presentations was necessary to collect the data for the INDSCAL and hierarchical clustering (HCA) analyses, 60 practice trials balanced for visual field were initially presented to allow subjects to become familiar with the stimuli so as to reduce the possibility of practice effects on RT measures (Urcuioli, Klein & Day, 1981). The practice trials were followed by 360 experimental trials in 3 blocks of 120 presentations each.

3.3.3.3. Statistical Analyses

The data was analyzed by a special multidimensional scaling (MDS) procedure, the INDSCAL developed by Carroll and Chang (1970; for a general discussion of MDS procedures see Davison, 1983, and Kruskal & Wish, 1978) and a HCA. The input for INDSCAL is a group of n half-matrices (where n represents the number of subjects), or proximity matrices. For this study, each element in the half-matrix was a RT representing the category matching decision of two animal names. This measure was found to be significantly positively correlated with independently judged degree of semantic similarity (e.g., Rips, Shoben & Smith, 1973). INDSCAL computes via an iterative process a group cognitive space that takes into account the individual differences in the saliency, or importance, of each dimension in organizing the space.

This is accomplished by assigning a weight index to each subject's dimensions, where a high weight index indicates that this dimension is important to the subject. INDSCAL also computes a skewness index, which is a measure of the distribution of saliency among dimensions, or the consistency with which a subject is using different dimensions. The skewness index varies between 0, for subjects with dimension weights proportional to the average weights, and 1, for subjects with one large weight and many low weights.

The purpose of the HCA is to successively fuse a number of concepts into groups. A cluster is defined as a set of contiguous elements, where concepts within the same cluster are more similar to each other than to concepts belonging in another cluster (Everitt, 1974, p. 43). The starting point of this procedure is a matrix of similarity data, as with INDSCAL. During successive stages, the method fuses concepts which are most similar (in the current study, pairs with fast RTs), into clusters, until finally all concepts are part of a single cluster. The stopping rule for the purpose of this investigation is the point where all concepts had been considered and assigned to a cluster (see Everitt, 1974, for a general discussion of clustering techniques).

3.3.4. Results

3.3.4.1. Traditional accuracy and RT analyses

RTs (RTs) greater than 2 seconds were regarded as misses. Repeated measures analyses of variance (ANOVAs) with stimulus type (animal vs. bird pairs) as the within-subjects variable and visual field as the repeated measure were performed for both RTs and the number of correct responses. The repeated measures ANOVA of RTs revealed a significant main effect of visual field ($F(1,38) = 34.13$, $p < .0001$) but not

of stimulus type ($F(1,38) = 1.76$; $p = .19$) and a significant interaction ($F(1,38) = 4.84$; $p < .05$). The significant interaction may have been due to the particularly poor performance in the LVF/RH on bird pairs (see Table 7). Post-hoc comparisons (paired two-tailed t-tests) confirmed that all pairs, animal pairs alone and bird pairs alone were responded to quicker in the RVF/LH than in the LVF/RH ($t(19) = 5.43$; $p < .0001$; $t(19) = 2.99$; $p < .01$; and, $t(19) = 5.07$; $p < .0001$, respectively). A repeated measures ANOVA of the number correct resulted in significant main effects for both visual field ($F(1, 38) = 44.94$; $p < .0001$) and stimulus type ($F(1,38) = 10.63$; $p < .01$) but no significant interaction. Post-hoc comparisons confirmed that significantly more correct responses were made to all pairs, animal pairs alone and bird pairs alone in the RVF/LH compared to the LVF/RH (all $p < .001$) and that significantly more animal pairs were correctly identified than bird pairs in both the LVF/RH and RVF/LH ($t = 4.36$; $p < .001$ and $t(19) = 3.78$; $p < .01$, respectively). Importantly, the number of correct category matching decisions was greater than chance in both the LVF/RH and RVF/LH (66.25/90; $t(19)= 7.98$; $p < .0001$ and 76.55/90; $t(19) = 16.66$; $p < .0001$, respectively), indicating that the RH was capable of performing the task, although with less competence than the LH. The following analyses were performed with the animal data only.

Table 7. Means ± Standard Deviations of RTs and Number of Correct Responses to Animal + Bird Pairs, Animal Pairs, and Bird Pairs in the LVF/RH and RVF/LH.

	LVF/RH		RVF/LH	
	RT	Number Correct	RT	Number Correct
animal + bird pairs (n = 90)	970 ± 117	66 ± 11	930 ± 116	76 ± 8
animal pairs (n = 45)	943 ± 123	36 ± 5	914 ± 115	40 ± 2
bird pairs (n = 45)	1011 ± 123	29 ± 8	948 ± 129	35 ± 6

3.3.4.2. Individual Differences Scaling Model (INDSCAL)

The input for INDSCAL were 20 10x10 half-matrices of RT data from decisions made in the LVF/RH and 20 10x10 matrices with RT data from RVF/LH decisions. The stress values, measurements of the amount of error in the INDSCAL solutions, were .26 and .27 for the two-dimensional LVF/RH and RVF/LH solutions, respectively. The amounts of variance of the original data accounted for by the two-dimensional LVF/RH and RVF/LH INDSCAL solutions were not significantly different (r^2 means and standard deviations were .65 ± .11 and .62 ± .08, respectively; $t(19) = 1.08$; $p = .29$), indicating that the INDSCAL procedure could scale the RT data from both visual fields equally well. Moreover, the skewness indices, measures of how consistently subjects employed the dimensions, were not significantly different between LVF/RH and RVF/LH INDSCAL solutions ($t(19) = 0.22$; $p = .83$).

Table 8. Means and Standard Deviations of Amounts of Variance of Original Data Accounted for (r^2), Skewness Indices and Dimension Weights of the 2- and 3-Dimensional LVF/RH and RVF/LH INDSCAL Solutions.

	LVF/RH Mean ± SD	RVF/LH Mean ± SD
2-dimensional solution:		
r^2	.65 ± .11	.62 ± .08
Skewness Index	.14 ± .12	.13 ± .11
Dimension 1 weights	.61 ± .10	.58 ± .07
Dimension 2 weights	.51 ± .09	.52 ± .09
3-dimensional solution:		
r^2	.73 ± .10	.62 ± .06
Skewness Index	.23 ± .08	.22 ± .11
Dimension 1 weights	.62 ± .12	.51 ± .10
Dimension 2 weights	.46 ± .10	.50 ± .09
Dimension 3 weights	.32 ± .11	.30 ± .11

A different pattern emerged within each solution with respect to the relative importance of each dimension, or dimension weights. Paired, two-tailed t-tests revealed a significant difference in the dimension 1 and dimension 2 weights for the LVF/RH solution ($t(19) = 2.85$; $p = .01$), indicating that dimension 1 was more important in the conceptual organization than dimension 2, whereas RVF/LH dimension 1 and 2 weights were not significantly different ($t(19) = 1.75$; $p = .10$), indicating that both dimensions were of equal relevance in conceptual organization.

In order to further elucidate the distribution of weights among dimensions, three-dimensional INDSCAL solutions were calculated. The stress values for three-dimensional LVF/RH and RVF/LH INDSCAL solutions were .22 and .26, respectively. The LVF/RH solution accounted for significantly more variance of its original data than the RVF/LH solution ($t(19) = 4.64$; $p < .001$). In fact, a comparison of two- and three-dimensional r^2 revealed that the LVF/RH data benefited from the addition of an additional dimension ($t(19) = 5.98$; $p < .0001$) whereas the RVF/LH data did not ($t(19) = 0.31$; $p = .76$). The skewness indices of LVF/RH and RVF/LH solutions were not significantly different ($t(19) = 0.37$; $p = .71$), indicating again that the subjects used the dimensions equally consistently. As only the LVF/RH data benefited from the additional dimension, only its dimension weights were subjected to further analyses. These revealed that dimension 1 was more important than both dimensions 2 and 3 ($t(19) = 3.75$; $p < .01$ and $t(19) = 6.25$; $p < .0001$, respectively) and that dimension 2 was more important than dimension 3 ($t(19) = 3.96$; $p < .001$; see Table 8).

3.3.4.3. Hierarchical Clustering Analyses (HCA)

The RT data from the tachistoscopic category matching task were averaged over subjects for each visual field and subjected to the HCA. The results for LVF/RH and RVF/LH data are shown superimposed on the respective two-dimensional INDSCAL solutions in Figure 14. LVF/RH data clustered into two groups: cluster 1 contained wolf, lion, cat, dog, monkey, horse, and elephant and cluster 2 contained sheep, pig and tiger. The HCA could not reveal any coherent clusters from the RVF/LH data, thus, all animals were clustered into one group.

3.3.4.4. Post-hoc analysis of semantically associated animal pairs

Two words are said to be associatively related when one word is often produced in response to the other in a free word association test. Associative relationships are presumably based on the co-occurrence of two words in language and its processing takes place at the level of word form representation, as opposed to semantic

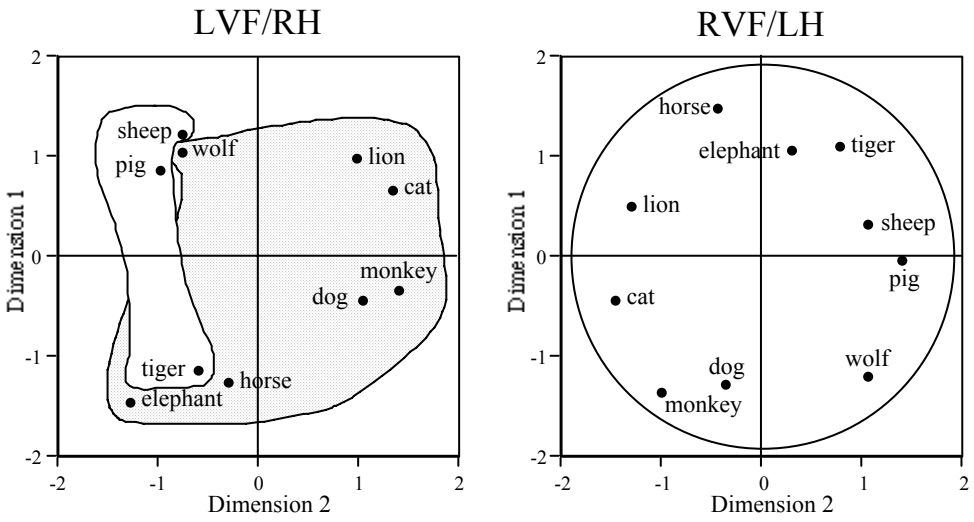


Figure 14. Two-dimensional INDSCAL solutions with superimposed HCA results for LVF/RH and RVF/LH category matching RT data from the unilateral category matching tachistoscopic task.

relationships, which are presumably based on categories and are processed at the level of meaning (Collins & Loftus, 1975; Chiarello, Burgess, Richards & Pollock, 1990). Because semantically similar word pairs may also be associatively related (e.g., “cat” and “dog”), recent studies have emphasized controlling for associative relationships when attempting to investigate semantic processes (e.g., Moss, Ostrin, Tyler & Marslen-Wilson, 1995).

Since the stimuli in the current study were chosen irrespective of the strength of associative relationships, post-hoc correlations of RTs with associativity (Kiss, Armstrong, Milroy & Piper, 1973; only 13/45 animal pairs were judged as associated) were calculated to indicate the influence of associative relationships on the category matching decisions. Both LVF/RH and RVF/LH RTs were not correlated with the strength of association (Pearson’s r = -.47; p = .11 and r = -.26; p = .40, respectively).

3.3.5. Discussion

A RVF/LH advantage emerged on the unilateral category matching task in terms of the number of correct responses and RTs. LVF/RH performance, however, was superior to chance, indicating that the RH also possesses competence in making category matching decisions. These results are comparable to those of Gross (1972) and Urcuioli et al. (1981), both of whom reported RVF/LH advantages in terms of RTs on their category membership tasks in addition to equal percent (Gross, 1972) or number of errors (Urcuioli, Klein & Day, 1981) in each visual field. It is interesting that similar findings emerged despite methodological differences; Urcuioli et al. always presented one category member foveally whereas in the present experiment both category members were presented laterally. Rather than suggest a RVF/LH dominance

for the current category matching task, however, we further carried out qualitative analyses which attempted to elucidate the processing mechanisms responsible for individual RTs.

A comparison of RH and LH INDSCAL solutions revealed that the INDSCAL model could scale LVF/RH RTs onto both two- and three-dimensional spaces. The dimension weights, or importance of each dimension, in the RH INDSCAL solutions were all significantly different from one another. The RVF/LH RT data could only be scaled onto two-dimensional space. These dimension weights, however, were not different from one another. Moreover, the low skewness indices in both the RH and LH INDSCAL solutions indicated that these patterns were consistent across subjects. Translated in terms of RTs, some animal pairs in the LVF/RH were consistently reacted to faster than other pairs, whereas animal pairs presented to the RVF/LH consistently showed no such differentiation. These findings were supported by the HCA results, which revealed no discernible clusters from the RVF/LH RT data but two clusters from the LVF/RH RT data.

These present findings can best be explained by the depth of activation hypothesis of semantic processing. If, as Chiarello and her colleagues suggest (Chiarello, Burgess, Richards & Pollock, 1990), the RH slowly and diffusely activates a semantic network, one would expect RTs to stimuli presented in the LVF/RH to be slow but to benefit from an overlap of activation for semantically related concepts (Collins & Loftus, 1975). The LH, which presumably quickly and focally activates the semantic network, would produce the opposite pattern, namely fast RTs without the benefit of an overlap of activation. This pattern is reflected in the mean RTs and INDSCAL solutions from each visual field.

An alternative explanation might maintain that the RH was not capable of performing this task and thus the RH INDSCAL solution reflected this incompetence, or that the category matching task was simply too easy for the LH. We believe that the former interpretation is unlikely because a) the number of correct responses in the LVF/RH was significantly greater than expected from chance and b) the skewness indices of both the two- and three-dimensional RH INDSCAL solutions were low, indicating that the RTs were consistent across subjects. The latter interpretation is consistent with Chiarello et al.'s (1990) processing hypothesis; quick and focal activation of concepts leads to efficient, albeit less differentiated, responses.

A note is needed on two possible confounding experimental variables in our experiment: semantic associativeness and category dominance. The processing of associative relationships is thought to take place at the lexical representation level of words and be dependent on the co-occurrence of words in language, whereas the processing of semantic relationships is thought to take place at the semantic, or meaning level (Moss, Ostrin, Tyler & Marslen-Wilson, 1995). Thus, stimulus pairs related associatively as well as categorically may not reflect "pure" semantic processing. Moreover, Drews (1987) found a greater RH competence for associated over categorical stimuli and the reverse pattern in the LH. A post-hoc analysis of the influence of associative strength on RTs in both visual fields, however, revealed no significant relationships.

Hines, Czerwinski, Sawyer and Dwyer (1986) found RH priming with categorically related primes only when these primes were within the first few most dominant exemplars. The stimuli employed in the current experiment spanned the first thirty most often produced animals in an association task (Mannhaupt, 1983) and thus category dominance is unlikely to have affected performance.

The present study found that both the LH and RH exhibited competence for a unilateral category matching task. However, RVF/LH performance was faster than LVF/RH performance. A qualitative analysis of RTs indicated that the slower LVF/RH performance may have been due to its preferred processing style: the RH may slowly and diffusely activate semantic concepts, leading to slower but more differentiated responses. The LH, on the other hand, may quickly and focally activate semantic concepts, leading to fast but less diverse responses. Thus, RH performance would only be 'inferior' if speed were the criterion of success. It may be valuable for future tachistoscopic studies to consider the qualitative aspects of hemispheric performance before prescribing a fixed pattern of hemispheric dominance for language.

4. General Discussion

4.1. Language in the “Right” Hemisphere

The studies reported here investigated three aspects of RH semantic language ability: 1) the influence of task demands on measures of RH semantic competence (Study 3.1.); 2) the functional neuroanatomical contribution of the RH to "pure" semantic processing (Study 3.2.); and, 3) qualitative aspects of RH semantic processing (Study 3.3.). Each contributed in small part to the delineation of factors which determine when, how, and under which circumstances RH semantic language processing takes place.

4.1.1. Asking the "Right" Question

Study 3.1. confirmed that, in general, the LH solves orthographic verbal tachistoscopic tasks more accurately than the RH. In tachistoscopic tasks, in which the stimulus quality is degraded by the very short exposure times (i.e., data-limited conditions[8]), accuracy measures presumably reflect whether or not the stimulus information was able to reach the cognitive processing system (Norman & Bobrow, 1975; Santee & Egeth, 1982; see also Babkoff & Faust, 1988). Thus, the LH perceptual system clearly appears better equipped to process orthographic verbal information than that of the RH. RT measures under data-limited conditions, on the other hand, purportedly reflect limitations not of the perceptual, but of the cognitive system (Norman & Bobrow, 1975; Santee & Egeth, 1982). In other words, accuracy scores measure

access to the cognitive system, while RTs measure *processing in* the cognitive system. Study 3.1. thus also replicated the well-established finding that the LH is more efficient than the RH making lexical decisions (Mishkin & Forgays, 1952; Bradshaw, 1989), as evidenced by its overall faster RTs. However, both hemispheres were equally competent (in terms of RTs) at making (explicit) semantic decisions.

Study 3.1. also investigated the influence of implicit and explicit task demands on hemispheric semantic processing. The extent of semantic processing could be measured in both conditions since each presented the hemispheres the *same stimuli* – closely and distantly semantically related category exemplars – and tested for the existence of semantic distance effects (i.e., faster RTs to closely compared to distantly related category exemplars; Rips, Shoben & Smith, 1973). The results illustrated that the semantic content of the stimuli was not appreciated in the implicit semantic condition (LDT), whereas the semantic information was processed in *both hemispheres* to the *same extent* in the explicit condition (SDT). The methodological implications for studies of hemispheric semantic processing are clear: since divided visual field priming paradigms (Zaidel, White, Sakurai & Banks, 1988) and bilateral (Boles, 1990; Olk & Hartje, 2001) or foveal-lateral (Chiarello, Burgess, Richards & Pollock, 1990) displays measure information processing of and interactions between both hemispheres, the most valid paradigm to measure the individual hemisphere's semantic ability is the *non-priming divided visual field paradigm with unilateral displays which demand an explicit semantic decision*.

---

[8] According to the distinction drawn by Norman and Bobrow (1975), tachistoscopic paradigms can be considered data-limited processing tasks. That is, the quality of the stimulus is diminished by the very brief exposure durations, and performances presumably reflect whether or not the stimulus information reached the cognitive processing system. Here, both perceptual and cognitive factors are important. Data-limited tasks are contrasted with resource-limited tasks, i.e. those in which the quality of the stimulus is intact (e.g., long exposure durations) such that performances reflect the actual capacity of the cognitive processing system. Perceptual factors are therefore not critical, as the stimulus is unhindered in its way to

These findings exemplify the multifactorial and dynamic nature of the concept of hemispheric asymmetry. The LH is not simply dominant for language processing; e.g., it dominates lexical, but not semantic processing - but not always. For example, a LDT with non-orthographic and syllabic-ideographic stimuli (stenography) elicits a LVF/RH advantage (Regard, Landis & Graves, 1985; see also Regard, Landis & Hess, 1985), whereas a LDT with verbal semantic information elicits a RVF/LH advantage. Hemispheric asymmetr*ies* depend on the question asked, and not just the nature of the stimulus; with constant stimulus input, they dynamically adapt themselves to the various factors defining the nature of the task.

4.1.2. Quantifying the Hemisphere's Semantic Answers

The purpose of Study 3.2. was to quantify the contribution of the RH to "pure" semantic processing in healthy individuals. This was to be a first step in the study of the functional neuroanatomical foundations of the RH language systems, which would then best be studied with an event-related design. Previous functional imaging studies with healthy individuals had found no or only minimal RH activation during semantic processing, results at odds with the wealth of evidence from investigations with brain-damaged populations (see Section 2.2.). We theorized that these negative findings were the consequence of their employment of lexicosemantic target tasks with orthographic or phonological baseline tasks. Such subtraction methodologies resulted in combined lexical and semantic activations, which disadvantaged the lexically less competent RH. To test this hypothesis, paradigms were constructed and a subtraction

---

the cognitive system; rather, cognitive capacity limits performance (Norman & Bobrow, 1975).

procedure adopted to individually target lexical and semantic processes and to quantify each hemisphere's contribution to each. A second possible reason for the lack of significant RH functional activations in previous functional imaging studies of semantic processing may have been their adoption of region of interest (ROI) analyses. These were based on known LH language systems and assumed homotopic organizational principles. The LH, however, may have a more modularized functional organization than the RH (Semmes, 1968; Fiez & Petersen, 1998; Zaidel et al., 2000).

The results of Study 3.2. supported a LH functional dominance for "pure" lexical processing (localized in the left inferior parietal lobe) and a shift to RH functional dominance during "pure" semantic processing (localized at fronto-temporal sites). The left fronto-temporal activations already evidenced in the lexical subtraction indicate that the semantic task called upon bilateral fronto-temporal functions. Importantly, these findings could be demonstrated because no *a priori* assumptions were made about the localization of language functions in the RH (i.e., no ROI analyses were undertaken); if e.g. only middle temporal lobe semantic activations in each hemisphere are compared, an overall LH functional dominance results. Thus, not only was significant RH functional activity evidenced during "pure" semantic processing, but this activity appeared to be more diffusely spread than the LH activity. These findings are consistent with a diffuse functional organization in the RH and modular functional organization in the LH (Semmes, 1968).

4.1.2.1. Neuroanatomical Evidence for a Modular (LH) - Diffuse (RH) Organization of Function

One connectionist theory derived from parallel distributed processing techniques attempted to model these hemispheric differences in functional organization (Woodward, 1988). This model suggested that the LH is dominated by highly coupled, non-overlapping connections between vertical cortical columns, particularly suited for the exact encoding of small differences. The RH, on the other hand, is hypothesized to depend on overlapping, horizontal axonal collaterals with greater distances between neuronal populations (see Figure 15). Neuroanatomical and neurophysiological support for this theory has been lacking (Springer & Deutsch, 1998). However, Galuske et al. (2000) recently conducted a neuronal tract tracing study on postmortem brains which yielded striking results. These authors quantified the size of labeled cell clusters and inter-cluster distances in posterior

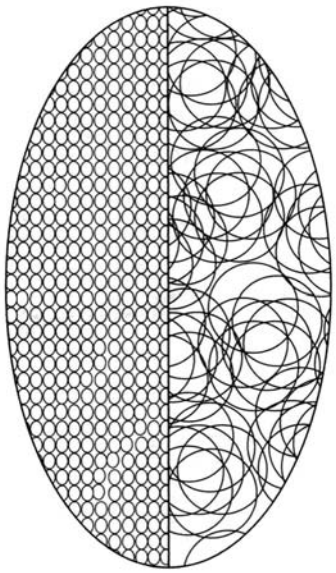


Figure 15. A connectionist theory of functional hemispheric organization (Springer & Deutsch, 1998, p. 322).

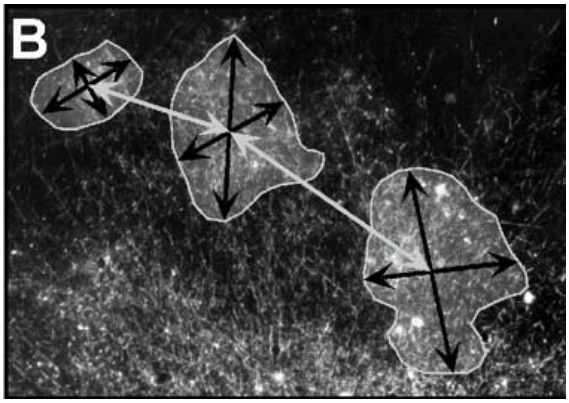


Figure 16. Clusters of labeled cells axon terminals with black arrows depicting cluster diameters and gray arrows inter-cluster distances (Galuske et al., 2000, p. 1948).

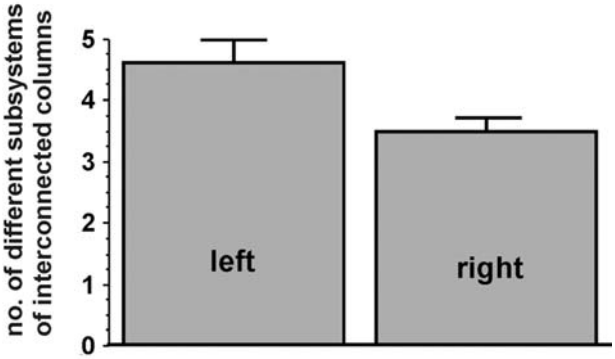


Figure 17. Estimated number of different subsystems of interconnected columns in area 22 of LH and RH (Galuske et al., 2000, p. 1949).

area 22 of both hemispheres (see Figure 16). Although cluster diameters were similar in both hemispheres, inter-cluster distances were circa 20% longer in the LH than in the RH. That is, RH neuronal populations overlapped more in the RH than in the LH, corresponding to a greater number of independent subsystems in the LH than in the RH (see Figure 17; Galuske, Schlote, Bratzke & Singer, 2000). A modular LH and diffuse RH organization of function accounts not only for the findings in Study 3.2., but also for the lack of striking semantic deficits following circumscribed RH lesions. Moreover, as described in the next section, this organization is functionally compatible with a focal activation of the semantic network in the LH and a widespread semantic network activation in the RH.

4.1.3. Dynamic Semantics in the Hemispheres

Study 3.3. investigated the qualitative nature of RH semantic processing. Specifically, given a RH semantic competence and the conditions under which it is best studied, how does the RH actively process conceptual information? The competing theories tested were: 1) the depth of activation hypothesis, which postulates that the LH rapidly and focally and the RH slowly and diffusely activates the semantic network (Chiarello, Burgess, Richards & Pollock, 1990; Beeman et al., 1994), and 2) the time-course hypothesis of semantic activation, which hypothesizes that both closely and distantly semantically related information are initially available to both hemispheres, but that distantly related information becomes suppressed in the LH later in the time course of semantic activation (Burgess & Simpson, 1988; Koivisto, 1997; see Section 2.3.). A non-priming, divided visual field paradigm was employed with unilateral presentations of two category exemplars. To measure the extent of semantic activation (i.e., focal or diffuse), Study 3.3. took advantage of the semantic distance effect described in Study

3.1., namely the phenomenon that closely related category exemplars are reacted to faster than those that are distantly related (Rips, Shoben & Smith, 1973). In contrast to Study 3.1., where stimulus pairs were *a priori* divided into closely and distantly related category pairs, Study 3.3. employed an INDSCAL (Carroll & Chang, 1970) to construct semantic networks from the category matching RT data from each hemifield. Semantic networks, or spaces, from each hemifield/hemisphere were thus attained and their resultant indices statistically compared: amount of variance of original RT data accounted for by the scaled solution (r^2; goodness of fit; validity); skewness indices (i.e., the consistency with which the individual subjects used the dimension; reliability); and, dimension weights (interpreted as the importance of a given dimension to the organization of the network). We investigated whether 1) the INDSCAL solutions from each hemifield/hemisphere were valid (by judging the goodness of fit, r^2) and 2) reliable (i.e., how consistently the subjects used the dimensions) and 3) how differentiated the structure of each hemifield/hemisphere's INDSCAL solutions were (i.e., the number of dimensions of significantly differing weights). Since more diffuse activation of the semantic network results in more semantic features being activated (Collins & Loftus, 1975), we hypothesized that a focal activation of the semantic network would result in an INDSCAL solution with few distinct dimensions and that a diffuse activation of the semantic network would result in an INDSCAL solution with many distinct dimensions.

Study 3.3. found that INDSCAL solutions from both LH and RH RTs were valid and reliable, but that the resultant semantic networks differed significantly with respect to the number of distinct dimensions: whereas the LH RTs could only be scaled into a two-dimensional space of equal dimension weights (i.e., no distinct hierarchy), RH RTs could be scaled into a three-dimensional space, with all three dimensions differing significantly. These findings correspond to a focal LH and diffuse RH network activation,

and thus support the depth of activation hypothesis of hemispheric semantic processing (see also Hagoort, Brown & Swaab, 1996). The implications of these qualitative differences in hemispheric semantics will be explored in more detail below.

4.2. A Day in the Life of Two Hemispheres

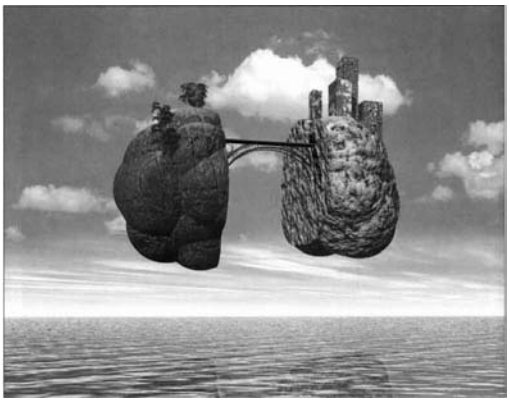


Figure 18. *Two Worlds* (Carter, 1999, p. 34).

The studies described above considered the two hemispheres as separate worlds, neglecting their incessant daily interactions across the largest bundle of fibers in the human brain, the corpus callosum. Three main models have been forwarded to describe how the hemispheres communicate: 1) the callosal relay model, 2) the relative efficiency (Moscovitch, 1986), or direct access (Zaidel, 1983), model, and 3) interactive models of which Cook's (1986) homotopic callosal inhibition theory (Cook, 1986) will be discussed (see Zaidel, 1983, and Bradshaw, 1989, for reviews).

4.2.1. Callosal Relay Model

The callosal relay model postulates that only one hemisphere is specialized for a given cognitive task. If information is sent to an incompetent hemisphere, it must be transferred (i.e., relayed across the corpus callosum) to the competent one. The result

is a degradation in stimulus quality and increase in RTs following presentations to the incompetent visual field. Figure 19 depicts the hypothesized performances of each hand following stimulations to each visual field in a verbal, presumably LH-dominant task. Overall, RVF responses will always be faster than LVF responses because the verbal information presented to the LVF must cross the corpus callosum. The transcallosal transmission time will also result in faster right than left hand RTs following RVF and LVF stimulations (main effects of visual field and hand; Zaidel, 1983; Bradshaw, 1989).

4.2.2. Relative Efficiency Model

The relative efficiency (Moscovitch, 1986), or direct access (Zaidel, 1983), model, on the other hand, purports relative degrees of specialization for any given cognitive

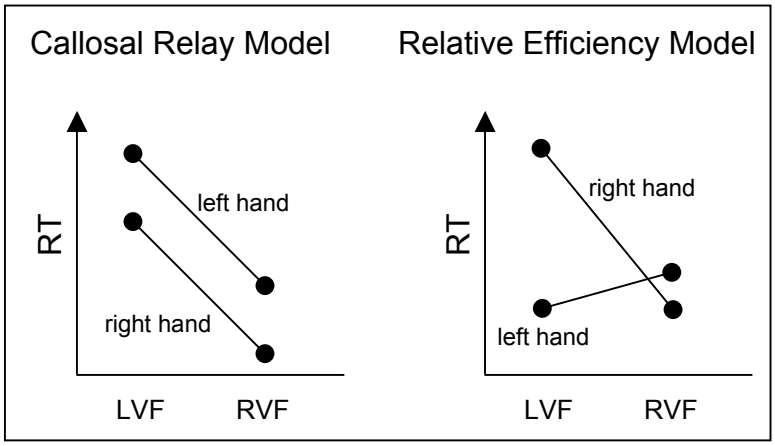


Figure 19. Hypothesized left and right hand RTs following LVF and RVF presentations of verbal stimuli according to the direct access and callosal relay models (adapted from Bradshaw, 1989, p. 113).

task (Bradshaw & Nettleton, 1981). Thus, performances in divided sensory field studies presumably reflect the relative ability and adopted processing strategy of the hemisphere first, 'directly', accessed (see Figure 20). For example, consider a verbal task for which the RVF/LH performances are typically superior to those in the LVF/RH. Although RVF/LH RTs will be faster overall (over both hands), this main effect of visual field will be modified by response hand because the responding motor information must

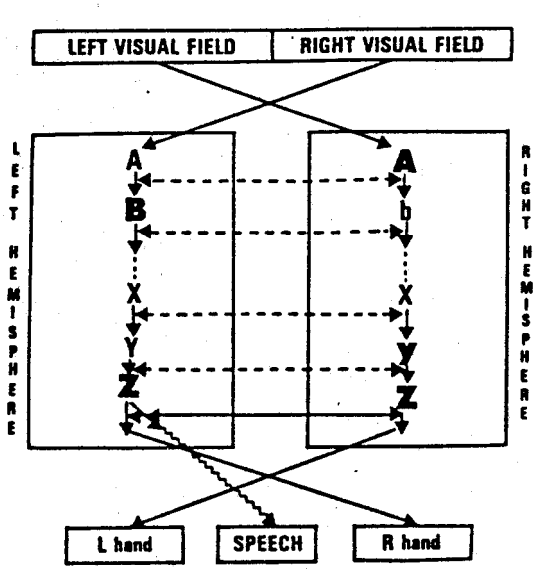


Figure 20. Relative efficiency (direct access) model of hemispheric functioning. Font thickness is correlated with relative efficiency for each component process of the task. Here, transcallosal transmission is first relevant at the motor output stage (Moscovitch, 1986, p. 95).

cross the corpus callosum. Thus, the RT advantage of a superior LH verbal performance will decrease with crossed, left hand responses, and the RT disadvantage of inferior RH verbal performance will be ameliorated with uncrossed, left hand responses, resulting in a significant interaction (see Figure 19; Zaidel, 1983; Bradshaw, 1989).

The callosal relay model was the logical interpretation of the striking language deficits following LH lesions and the comparably quite subtle impairments in semantic, metaphoric and prosodic language after RH injury. The findings from callosotomy patients and divided visual field studies with healthy subjects, however, suggested a significantly greater RH language competence. Moreover, analyses of RT responses of each hand in divided visual field tasks have consistently revealed visual field x hand interactions (Zaidel, 1983). Both facts support the relative efficiency model. How, then, can the lesion findings be reconciled with those from callosotomy patients and divided visual field studies? One solution may be the more diffuse organization of language function in the RH, as outlined in Section 4.1.2.1. Another may be that the LH

transcallosal inhibition of the RHs of callosotomy patients and presumably those of healthy subjects undergoing divided visual field stimulations are reduced (Regard, Cook, Wieser & Landis, 1994). The involvement of the corpus callosum in hemispheric functioning plays a vital role in interactive models such as the homotopic callosal inhibition model (Cook, 1986).

4.2.3. Homotopic Callosal Inhibition Model

The homotopic callosal inhibition model (Cook, 1986; see also Cook & Beech, 1990 and Wey, Cook, Landis, Regard & Graves, 1993) is based on neuroanatomical evidence that transcallosal fibers are primarily inhibitory and homotopic in nature. Thus, the hemisphere particularly suited to a given task (i.e. with the relatively greater efficiency; direct access model) will inhibit the activation of the same functions at homotopic sites in the opposite hemisphere. Importantly, surrounding areas in the inhibited cortex are active (see Figure 21), such that the opposite hemisphere is capable of processing other aspects of the information and ensuring a complementarity of hemispheric functioning as in the denotative (LH) - connotative (RH) dichotomy (Brownell, 1988). The model predicts that unilateral damage will "release" the opposite hemisphere from inhibition such that its performance on tasks for which it was previously less efficient will improve (Landis, 1987).

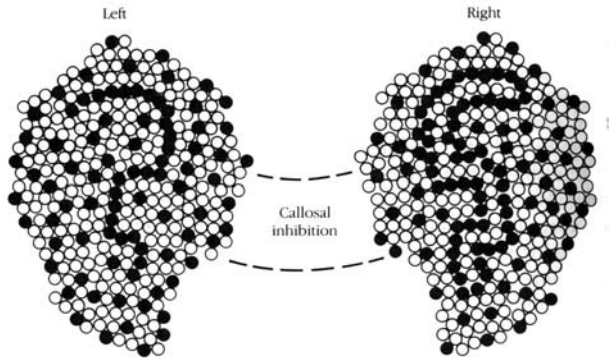


Figure 21. Homotopic callosal inhibition model (Cook, 1984, p. 200).

This model has since received experimental support from several studies. For example, Regard and colleagues (Regard, Cook, Wieser & Landis, 1994) performed divided visual field lexical and/or facial decision tasks in three patients with left and one with right unilateral limbic seizures. Seizure activity was bilaterally monitored with implanted stereotactic EEG depth electrodes or foramen ovale EEG electrodes. In general, unilateral seizure activity disrupted the corresponding hemisphere's functioning on the task for which it was presumably specialized (i.e., LH - LDT, RH - facial decision task; see also Regard, Landis, Wieser & Hailemariam, 1985). Strikingly, the disruption of RVF/LH LDT performance by left limbic seizure activity in patient C was associated with a concomitant *increase* in LVF/RH LDT performance; the RH appeared to be released from the LH's inhibition (see Figure 22; Regard, Cook, Wieser & Landis, 1994). Further support for the homotopic callosal inhibition model was provided by findings of a significant relationship between semantic paralexia production and lesion size in aphasics (Landis, Regard, Graves & Goodglass, 1983; see also Landis, 1987, and Regard & Landis, 1984, and see Marshall & Patterson, 1983, for an alternative interpretation of the patient data), by divided visual field verbal priming experiments with healthy control subjects (Wey, Cook, Landis, Regard & Graves, 1993) and non-lateralized and lateralized mental rotation tasks with healthy subjects (Cook, Früh, Mehr, Regard & Landis, 1994). The integrated findings thus suggest that hemispheric functioning can best be modelled as a combination of direct access and interhemispheric interaction (Bradshaw, 1989). The consequence of transcallosal homotopic inhibition is an increase in efficiency; identical processing in the opposite hemisphere is inhibited such that other, possibly supportive processing can take place.

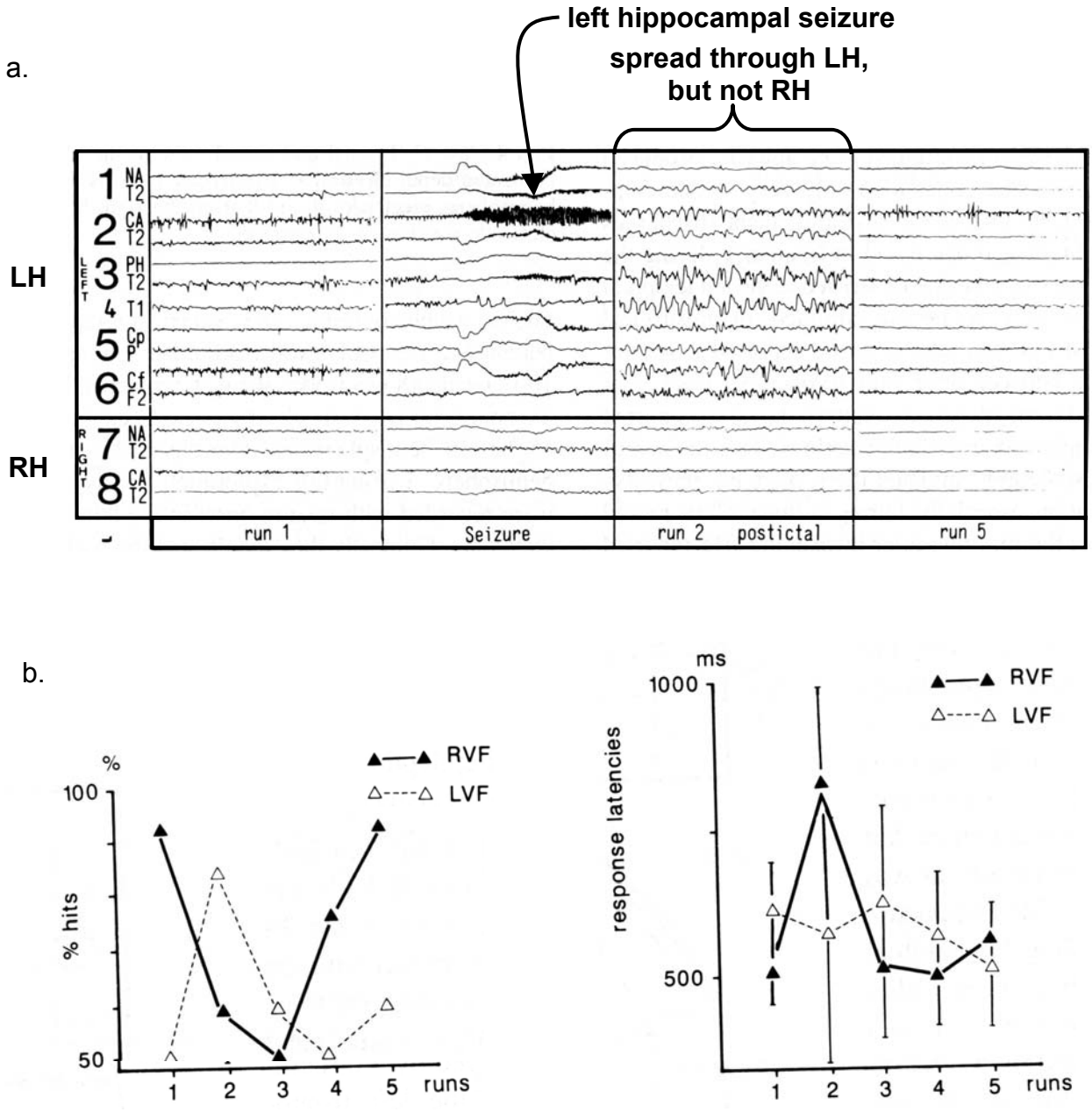


Figure 22. a) EEG recordings of pre-seizure, seizure, and postictal activity in a patient with unilateral left limbic seizures confirming left hippocampal seizure origin and spread of seizure activity to other LH, but not RH sites. b) Hemispheric performances on a divided visual field lexical decision task synchronous to the EEG activity; the right visual field/LH advantage shifts to the left visual field/RH (in terms of hit percentage and RTs) during the left limbic seizure and its spread (adapted from Regard et al., 1994, p. 98).

4.3. The RH in the Clinic: Recovery from aphasia

The delineation of RH language systems is highly relevant to therapy programs for aphasic patients[9] which attempt to activate the language functions of spared, RH areas and positively influence functional-neuroanatomical reorganization (Nudo, Wise, SiFuentes & Milliken, 1996). For example, based on the findings that the RH is primarily responsible for the stress, intonation and melody of language, Melodic Intonation Therapy (MIT) attempts to activate these spared functions in aphasic patients[10] by teaching them to intone normal language with exaggerated stress, rhythm and melody (Sparks, Helm & Albert, 1974). Not only "normal", but also *latent* RH language functions could be exploited in the recovery process (Selnes, 1999). Clearly, to be activated these latent functions must first be characterized, i.e. in situations where the RH is released from the LH's inhibitory control (e.g. following a LH lesion[11] or during a unilateral epileptic seizure, see Section 4.2.). In the last decade, studies of functional recovery from aphasia have increasingly employed functional imaging techniques to identify which regions, in particular those in the RH, are associated with the behavioral changes accompanying recovery (see Frackowiak, Friston, Frith, Dolan & Mazziotta, 1997, and Pizzamiglio, Galati & Committeri, 2001, for reviews). These have revealed that, in stroke patients, RH

Figure 23. *Aphasia* (S. Kranz, ©1999).

---

[9] For an overview, see Weniger & Springer, 2002.

[10] Belin et al. (1996) conducted a PET study with seven Broca's aphasia patients who had been successfully treated with MIT. Changes in relative cerebral blood flow during a word repetition task revealed significant activation in RH regions homologous to Broca's area, while exaggerated (i.e., melodically intoned) word repetition activated perilesional sites. These findings indicate that the neuroanatomy targeted by a rehabilitative treatment may not be that which is responsible for the recovery (Belin, Van Eeckhout et al., 1996).

[11] Also John Hughlings Jackson suggested that LH lesions affecting propositional speech could “heighten” the activity of the RH (Finger, 1994), p. 394.

involvement during recovery from aphasia depends both on the type of functional-neuroanatomical damage and, in particular, on the time post-stroke (Cappa & Vallar, 1992).

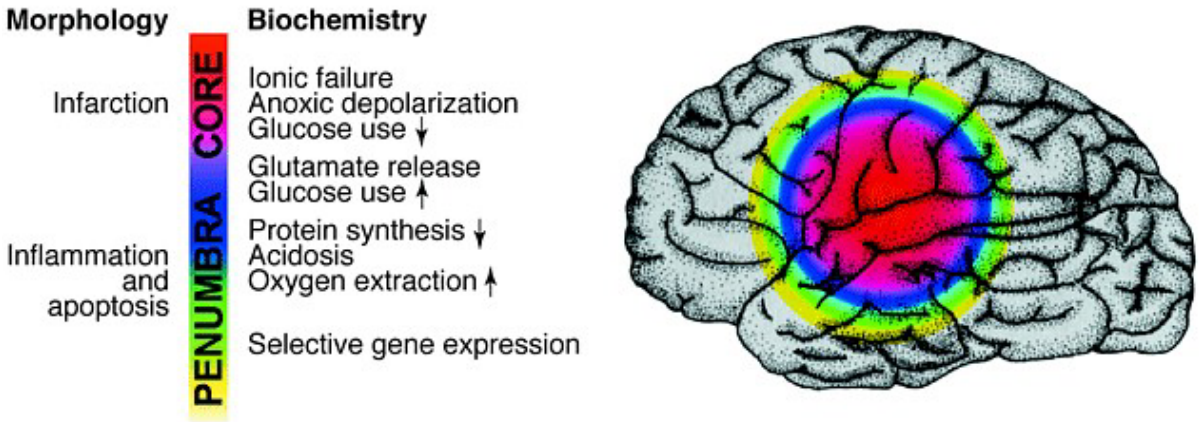


Figure 24. The ischemic penumbra (Dirnagl et al., 1999, p. 394).

4.3.1. Initial Recovery

Recovery of language abilities within the first weeks following ischemic infarction is related to the repurfusion in the affected LH areas as measured by changes in regional cerebral blood flow (Mimura, Kato et al., 1998) and regional glucose metabolism (Heiss, Kessler, Karbe, Fink & Pawlik, 1993). These functional changes may be attributable to the recovery of the penumbra, an area of critically ischemic and functionally impaired tissue surrounding the infarcted site (see Figure 24). With time, a portion of the outer penumbra recovers its function while the area concentric to and bordering the ischemic core infarcts (see Figure 25; Furlan, Marchal, Viader, Derlon & Baron, 1996; see also Heiss, 2000). Current imaging studies are attempting to measure blood perfusion in the penumbra to predict outcome and measure the efficacy of reperfusion drugs (Marchal, Benali et al., 1999).

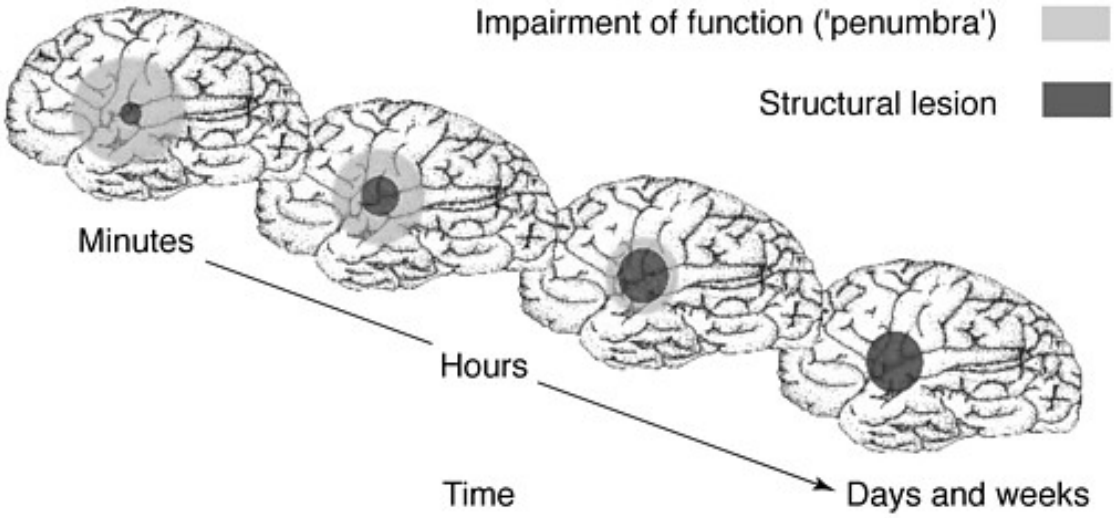


Figure 25. Recovery of the ischemic penumbra with time (Dirnagl et al., 1999, p. 396).

Imaging studies of behavioral recovery following LH stroke have focused on the *functional* activity in perilesional LH and spared LH and RH sites as well as their changes with time. Heiss et al. (1999) conducted a PET study of stroke patients tested two and eight weeks post-stroke. This study was lesion-based; patients were segregated into a frontal group (stroke in territory of the left anterior middle cerebral artery), a temporal group (stroke in territory of left posterior middle cerebral artery) and a subcortical group (infarcted regions in the basal ganglia, parts of subcortical white matter but no cortical lesions). In a group of healthy control subjects, a word repetition task compared to rest activated bilateral superior temporal, left precentral and left inferior frontal gyral sites (see Figure 26a; note: in contrast to the original article, control subject data is displayed in the same figure as the patient data). Compared to the control group, the subcortical group activated similar sites, the frontal group initially activated homologous RH regions and at follow-up bilateral sites, while the temporal group initially activated LH sites and at follow-up bilateral regions (see Figures 26b and c). However, improved language functioning in the combined subcortical and frontal

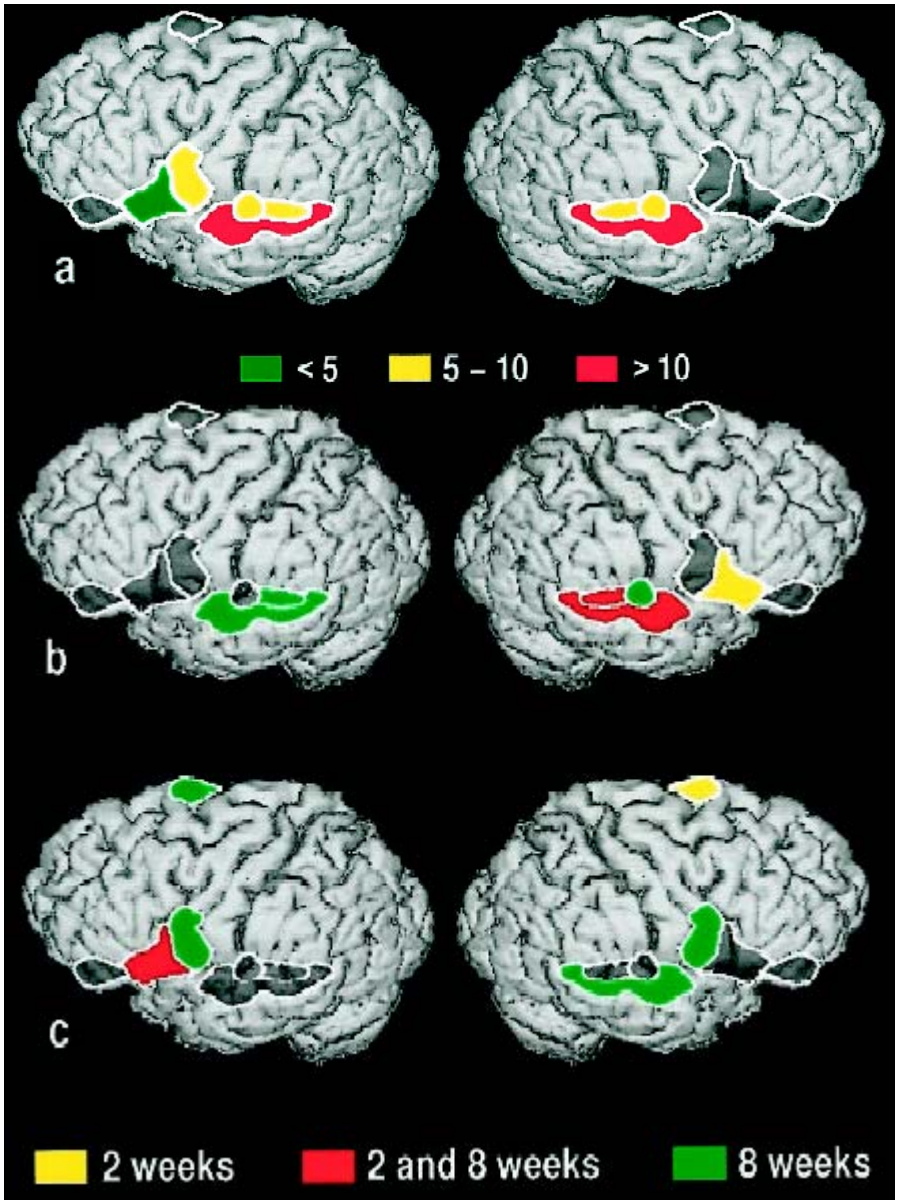


Figure 26. Sites of functional activity during a word repetition task (compared to baseline) in the control group (a) and in the frontal (b) and temporal (c) patient groups initially (2 weeks post-stroke) and at follow-up (8 weeks post-stroke) (dark regions represent nonsignificantly activation volumes of interest; adapted from Heiss et al., 1999, p. 435).

groups as measured by the Token Test (Orgass, 1982) was associated with initial left temporal functional activity (no such analysis was undertaken for the temporal group; Heiss, Kessler, Thiel, Ghaemi & Karbe, 1999). Similar results were reported by Ohyama et al. (1996): although right inferior frontal and posterior superior temporal regions were activated in a group of Broca's aphasics during a word repetition task compared to a rest baseline at least one month post-stroke, aphasia battery scores correlated only with

LH activity localized to, in contrast to Heiss et al. (1999), the inferior frontal lobe (Ohyama, Senda et al., 1996). These findings suggest that while the RH is recruited in the recovery process, optimal recovery of function may ultimately depend on the degree of spared LH tissue[12].

4.3.2. Late Recovery

This interpretation was amended by the findings of studies which investigated the relationship between long-term outcome and functional activity in aphasic patients. Cappa and colleagues (1997), for example, reported that improved language performance between 2 weeks and 6 months post-stroke was correlated with increases in glucose metabolism in RH, not LH, regions during the same period[13] (Cappa, Perani et al., 1997; see also Mimura et al., 1998, and Thulborn, Carpenter & Just, 1999). Weiller and colleagues (1995) investigated the functional correlates of recovered language ability in six Wernicke's aphasia patients. In this PET study, patients and healthy control subjects performed verb generation and pseudoword repetition tasks. In the healthy subjects, functional activity during the verb generation task compared to a rest baseline was documented mainly in the left lateralized superior and left middle temporal gyri as well as in the left inferior frontal gyrus, while pseudoword repetition compared to a rest baseline resulted in left lateralized superior temporal gyral activation (see Figure 27). Compared to the healthy control subjects, the recovered Wernicke's aphasics evidenced significantly more right superior temporal gyral and right inferior frontal activation on both tasks (see Figure 27; see also Cao, Vikingstad, George, Johnson & Welch, 1999 and Gold & Kertesz, 2000). Right superior temporal gyral

[12] In a patient with RH language dominance, recovery of language functions within circa 2 months following a RH stroke was also associated with RH, not LH, functional activity (Seghier, Lazeyras et al., 2001).

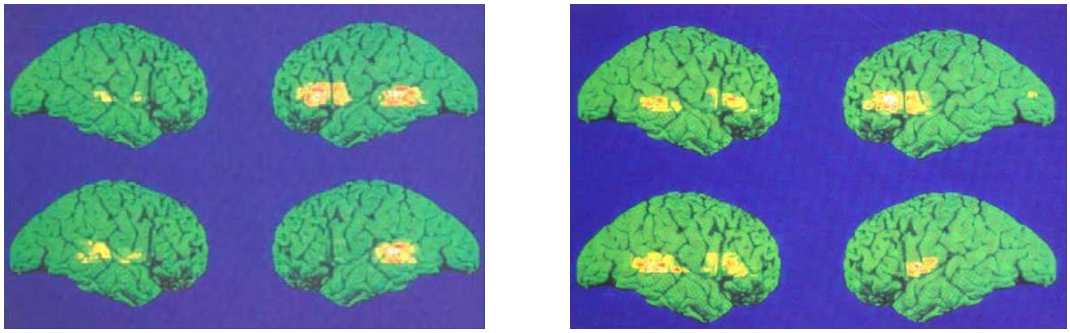


Figure 27. Functional activations in the control (left) and Wernicke's aphasia patient (right) groups during verb generation (top) and pseudoword repetition (bottom) compared to rest (Weiller et al., 1995, p. 728).

activation was also correlated with improved comprehension as measured by a short version of the Token Task during short term training with Wernicke's aphasics (Musso, Weiller et al., 1999).

Since articulate speech is relatively highly lateralized to the LH (compared to e.g. comprehension abilities; Bradshaw, 1989), it has been proposed that Broca's aphasia patients may be less likely than Wernicke's aphasics to recruit RH regions homologous to their LH lesions. This assumption was seriously challenged in a study by Rosen and colleagues (2000). Healthy control subjects and recovered Broca's aphasia patients performed a word-stem completion task (visual fixation baseline) during MRI scanning. The control subjects' functional activations were centered in the left inferior frontal and inferior temporal gyri. Broca's aphasia patients also significantly activated the left inferior temporal gyrus during the task, but their inferior frontal activity was located in the RH (see Figure 28, and, for similar findings in Broca's aphasia patients, see Silvestrini, Troisi, Matteis, Cupini & Caltagirone, 1995; Cao, Vikingstad, George, Johnson & Welch, 1999; and for similar findings in naming but not rhyming tasks, see Calvert, Brammer et al., 2000). Whereas the right inferior frontal activity in the Broca's aphasia patients in Rosen et al.'s (2000) study did not correlate with language performance, Cao et al.

---

[13] Cappa et al. (1997) interpreted their findings as the result of diaschisis, see Section 4.3.3.

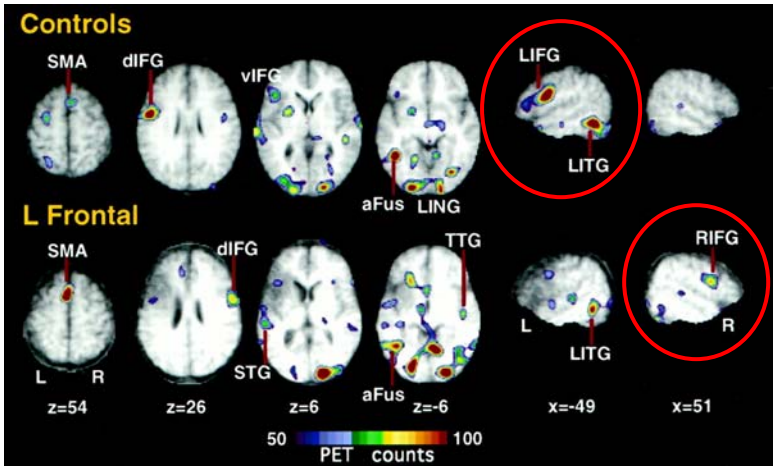


Figure 28. Functional activity measured with fMRI during a covert word stem completion compared to visual fixation baseline in the control and patient groups (adapted from Rosen et al., 2000, p. 1889).

(1999) reported that language recovery was associated with bilateral activity in their Broca's aphasia group (Cao, Vikingstad, George, Johnson & Welch, 1999). Thus, RH regions, in particular those homologous to the LH insult, appear to play a central role in the late stages of the recovery process in Wernicke's, Broca's as well as transcortical motor and sensory aphasias (Cao, Vikingstad, George, Johnson & Welch, 1999).

4.3.3. Transcallosal Inhibition (and Diaschisis)

The initial recovery of language functions (i.e. within first few months) is critically dependent on the amount of the ischemic penumbra that is recovered in the lesioned LH (Heiss, Karbe et al., 1997; Heiss, Kessler, Thiel, Ghaemi & Karbe, 1999). The RH, on the other hand, appears to play a central role in long-term recovery from aphasia. The stunning pictures provided by the functional imaging studies above thus support what has been known for over a century: the RH can assume language functions lost due to LH lesions (Gowers, 1887; Cappa et al., 1997). In light of the robust evidence from studies with healthy and callosotomy patients that articulation is strongly lateralized to the LH, the emergent RH inferior frontal activity in Broca's aphasia patients is astonishing and suggests that the RH possesses an impressive latent language ability

which may normally be suppressed by a mechanism of transcallosal inhibition described in Section 4.2.[14]. RH activity may not be apparent immediately following a LH lesion because of diaschisis, i.e. the gradually receding functional impairment at sites remote but anatomically connected to the lesion. Indeed, in a PET study by Cappa and colleagues (1997) found sites of significant functional hypometabolism in structurally unaffected regions in both the LH and RH of aphasic patients in the acute phase. The decreases in this hypometabolism were significantly correlated with increases in RH functional activity with time (Cappa et al., 1997).

Future functional imaging studies of recovery from aphasia will target the effects of training programs to determine which therapy for which behavioral deficit most optimally re-weights the language networks (Weiller et al., 1995; Weiller, 1998). The following methodological factors will significantly influence these findings: 1) not only patients preselected to perform the functional task (e.g. Warburton, Price, Swinburn & Wise, 1999), but also those who fail specific language tasks, should be investigated to identify the neural correlates of failed recovery; 2) functional imaging paradigms must be employed which measure the activity associated with recovered, spared (Pizzamiglio, Galati & Committeri, 2001) as well as non-recovered language functions; 3) based on considerations outlined in Section 2.3.2., region of interest analyses (e.g. Heiss, Kessler, Thiel, Ghaemi & Karbe, 1999) should be avoided as they may overlook significant RH contributions to language processing; 4) finally, analyses of functional data must also analyze sites of significant functional inhibition to better delineate the mechanisms of transcallosal inhibition and diaschisis. With respect to the last point, functional imaging methods could elucidate how balance of propositional (LH) and

[14] Although the RHs of most callosotomy patients do not develop the ability to speak, at least one such case has been described (Gazzaniga, Eliassen et al., 1996).

situational (RH) language processing found in the healthy brain changes as a result of circumscribed lesions.

4.4. Implications of the RH's Semantic Competence

4.4.1. Metaphors

> "Metaphor as a figure of speech has intrigued and stimulated scholars for thousands of years. Aristotle considered metaphor a sign of genius, believing that the individual who could make unusual connections was a person of special gifts. From that ancient tradition has emerged a working definition of metaphor: the capacity to perceive a resemblance between elements from two separate domains or areas of experience and to link them together in linguistic form." (Gardner, 1984)

Metaphor appreciation requires the understanding of the nonliteral, more distantly associated features of literal material. The first major indication of a RH involvement in metaphor appreciation was provided by Winner and Gardner in their seminal Brain article from 1977 (see Section 1.2.). Since, a slew of investigations have confirmed and extended these findings in unilaterally brain-damaged populations: RHBD patients have difficulties following indirect commands (Foldi, 1987; Weylman et al., 1989), in drawing inferences (Brownell, Potter, Bihrle & Gardner, 1986) and in grasping the nonliteral interpretations of short vignettes (Kaplan et al., 1990). Metaphor appreciation may also underlie the ability to understand humor. Indeed, RHBD patients, especially those with right frontal lesions (Shammi &

Figure 29. *Winter Thoughts* by Simon Fenwick, ©2001 Nature Reviews Neuroscience.

Stuss, 1999; see also McDonald, 1993), have difficulties understanding jokes (Wapner, Hamby & Gardner, 1981) or discerning the difference between ironic jokes and lies (Winner, Brownell, Happe, Blum & Pincus, 1998), and healthy subjects with high scores on a task thought to rely on RH mechanisms (i.e. a mental rotation task) rated jokes as funnier than those with lower mental rotation scores (no task associated with LH processes was however administered; Johnson, 1990).

Functional imaging methods with healthy subjects have supported the above findings. For example, an event-related potential study documented larger N400s[15] over the RH than the LH during the terminal words of metaphor sentences (Pynte, Besson, Robichon & Poli, 1996). In a functional transcranial doppler sonography study with healthy subjects, the strongly left-lateralized hemispheric perfusion during the presentation of literal verbal material was significantly reduced during the presentation of metaphoric material (Buchinger, Flöel et al., 2000). Finally, a positron emission tomography (PET) study of metaphor processing in healthy subjects reported significant RH prefrontal, temporal, precuneus, and anterior and posterior cingulate activations during the plausibility judgments of auditorily presented plausible and implausible metaphoric compared to plausible and implausible literal sentences (Bottini et al., 1994; see Figure 30). Interestingly, half of the sentences presented in the Bottini et al. (1994) study were developed to be nonsensical. Several functional imaging studies have demonstrated RH involvement during processing of incoherent language, e.g. sentences with semantic violations (Demonet, Celsis et al., 1992; Kuperberg et al., 2000; see also Caplan, 1995) and semantically anomalous verb-noun phrases (Min Kang, Constable, Gore & Avrutin, 1999). It remains to be tested whether the processing

[15] The first 200 msec of the ERP presumably reflects stimulus structuring, while the dip at circa 400 msec (N400) is inversely related to how expected the stimulus is (Pynte, Besson, Robichon & Poli, 1996).

of incoherent language is dependent on the same brain systems as those employed during metaphor comprehension; it is enticing to theorize that the same widespread semantic network activation characteristic of RH processing in general and metaphor

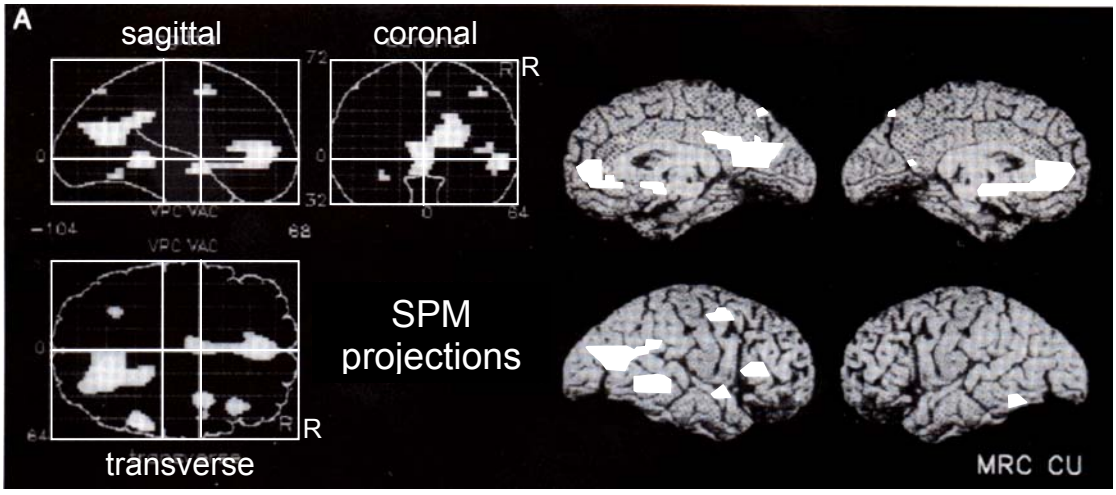


Figure 30. Functional activations as measured by PET during plausability decisions of metaphor vs. literal sentences (adapted from Bottini et al., 1994, p. 1249).

comprehension in particular is employed in the search to comprehend purportedly incomprehensible material.

The striking findings from unilaterally brain damaged patients and functional imaging studies with normal participants have not yet been conclusively confirmed in divided visual field studies with healthy subjects. In an implicit metaphor comprehension task, Faust and Weisper (2000) presented incomplete sentences as primes for laterally presented target words which represented either literally true, false or metaphoric endings to the prime sentence. Subjects decided following the presentation of the final, target word whether the completed sentences were literally true or false. Both RVF/LH and LVF/RH performances with metaphor sentences were inferior to those with literally false sentences, suggesting that both hemispheres were sensitive to the metaphoric material (Faust & Weisper, 2000). Anaki et al. (1998) employed a lateralized priming paradigm of lexical decisions with prime-target pairs which were either literally or

metaphorically related associates. At the short SOA (200 msec), lexical decisions to metaphorically related targets were facilitated in both hemifields / hemispheres. At the longer SOA (800 msec), metaphor associates were facilitated only in the LVF/RH and literal associates only in the RVF/LH (Anaki, Faust & Kravetz, 1998). As previously discussed (see Section 2.3.), the bilateral facilitation effects with metaphoric material may have been the consequence of the priming paradigm which presented the information to both hemispheres. Moreover, the metaphoric material presented in both studies actually consisted of idioms (e.g., "some nights are young", Faust & Weisper, 2000, p. 187, and "stinging-insult", Anaki, Faust & Kravetz, 1998, p. 353). Idioms are nonliteral phrases that are well-known and that, with time, acquire entries in the mental lexicon and are automatically processed as single words (Cacciari & Glucksberg, 1995; Gibbs, 1995; Tabossi & Zardon, 1995). Familiar metaphoric information such as idioms may induce qualitatively different hemispheric processing patterns compared to novel metaphoric stimuli (Tompkins, Boada & McGarry, 1992). Indeed, a recent study (Meier, 2002; Taylor, Meier, Brugger & Weniger, in press) supported this hypothesis. Healthy subjects performed a relatedness decision in a divided visual field experiment with unilaterally presented categorically, idiomatically and (novel) metaphorically related word pairs. Following the experiment, subjects rated the relatedness of each word pair according to a six-point Likert scale. Repeated measures analyses of variances of RTs failed to reveal a main effect of stimulus group or an interaction of stimulus group with hemifield. A different picture emerged, however, when only those word pairs were considered which the subjects considered related: RVF/LH responses to idiom pairs were significantly faster than those in the LVF/RH, but the common RVF/LH superiority with verbal (lexical) material disappeared with both categorically and metaphorically related stimuli (Meier, 2002; Taylor, Meier, Brugger & Weniger, in press; see Figure 31

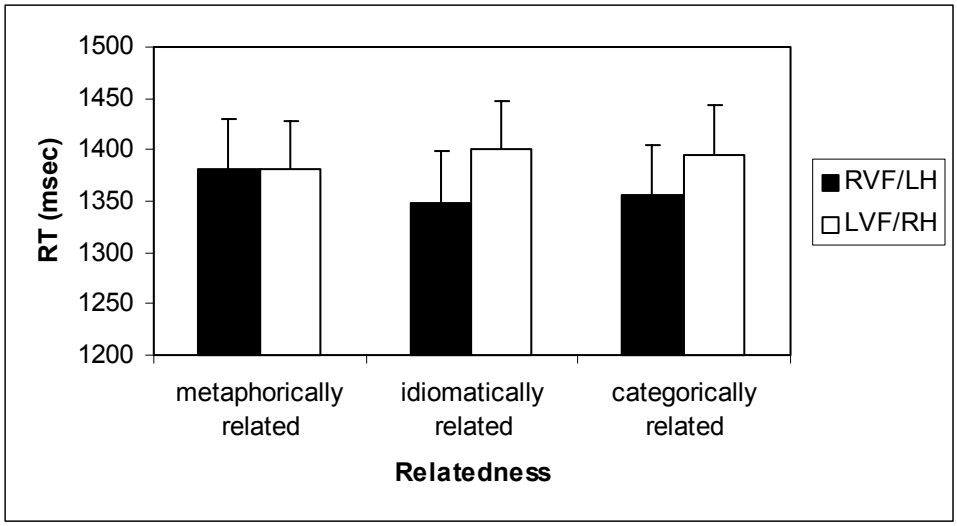


Figure 31. RVF/LH and LVF/RH RTs (with standard errors) to metaphorically, idiomatically and categorically related stimulus pairs judged as relatedin the post-hoc ratings.

and Rodel, Cook, Regard & Landis, 1992, for identical results with a relatedness decision of semantically associated stimuli).

A special role of the RH in metaphor appreciation and situational processing in general appears to be balanced by a the special ability of the LH to process denotative meanings. For example, a double dissociation of impaired denotative and spared metaphoric appreciation in LHBD and the reverse pattern in RHBD patients was evidenced in a sorting task (Brownell, Potter & Michelow, 1984; see also Brownell, 1988; Brownell, Simpson, Bihrle, Potter & Gardner, 1990 and see Tompkins, Boada & McGarry, 1992, and Van Lancker, 1987, for a failure to confirm these findings). This cooperative balance of function is consistent with the homotopic callosal inhibition model of hemispheric functioning (Cook, 1986): while the LH may "dominate" in the processing of linguistic forms and rules, there may be a complimentary RH dominance in processing nonliteral readings of linguistic expressions as required for novel metaphors or, as described below, in convergent thinking tasks.

4.4.2. Creativity

"... to produce through imaginative skill." (Merriam-Webster, 1998)

Psychological research into the basis of creativity has led to the conclusion that it must be multidimensional in nature. Mednick (1962) proposed three dimensions of creative thinking: 1) serendipity, or chance (see also Goldenberg, Mazursky & Solomon, 2001), 2) mediation, or convergent thinking (i.e., finding a relationship between apparently unrelated material), and 3) similarity, or divergent thinking (i.e. generating as many different ideas as possible starting from a given stimulus; Mednick, 1962). While a certain amount of serendipitous luck may be required for every creative act, convergent and divergent thinking are more likely to be founded on distinct neuropsychological processing mechanisms. Especially the production of a novel association between previously unrelated concepts (convergent thinking) appears well-suited to the diffuse semantic activation characteristic of RH processing (Leonhard & Brugger, 1998). Indeed, scores on the convergent Remote Associates Task[16] (RAT; Mednick & Mednick, 1967) were significantly associated with RH language capacity as measured by divided visual field (Weinstein & Graves, 2001; Weinstein & Graves, 2002) and dichotic listening (Weinstein & Graves, 2002) tasks. Similarly, a creativity index based

Figure 32. *Do you Like my Brain?* de Saint Phalle, 1971.

[16] In this task, subjects are presented with a list of word triads and are instructed to find a fourth word associated with all three stimulus words (e.g., stimulus: "rat - blue - cottage", possible answer: "cheese"; Mednick & Mednick, 1967).

on the Alternate Uses Test (Christensen, Guilford, Merrifield & Wilson, 1970) and the RAT (Mednick & Mednick, 1967) was associated with greater RH than LH EEG alpha activity (Martindale, Hines, Mitchell & Covello, 1984). Carlsson et al. (2000) split a group of healthy controls into high and low creatives based on a visuo-spatial convergent thinking task. During a generation task, regional cerebral blood flow as measured by PET was significantly increased in the RH of highly creative subjects compared to less creative subjects (see Figure 33; Carlsson, Wendt & Risberg, 2000). These findings confirm the significant role of the RH in convergent aspects of creative thinking.

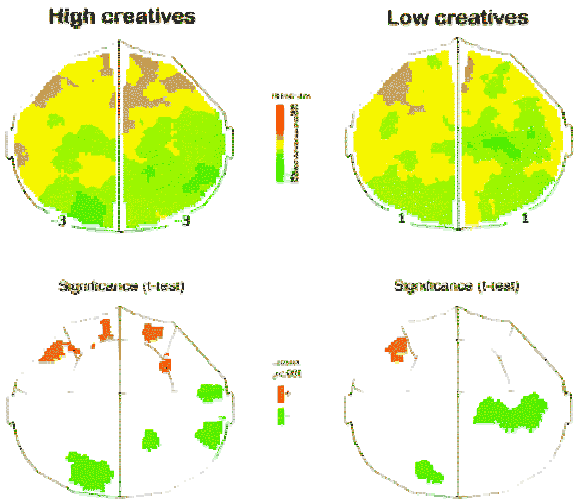


Figure 33. While less creative subjects evidenced primarily left frontal lobe activity, as expected, during the uses generation task compared to baseline, functional activity in the highly creative subjects was bifrontally distributed (Carlsson et al., 2000, p. 877).

RH activity, however, does not appear to be related to performance on tasks measuring divergent thinking, e.g. word fluency tasks (Poreh, Whitman & Ross, 1993-4; Weinstein & Graves, 2001; Weinstein & Graves, 2002). Instead, the interactive cooperation of both hemispheres may be required to successfully perform these tasks. Atchley et al. (1999) administered a test of divergent thinking (Wallach & Kogan, 1965) to healthy subjects who also underwent a divided visual field priming task. While both hemispheres of highly creative subjects primed subordinate word meanings of ambiguous word primes, only the RH of less creative subjects evidenced subordinate priming (Atchley, Keeney & Burgess, 1999), as expected (Burgess & Simpson, 1988). Thus, an interactive, or collaborative, model of

hemispheric functioning may best account for the ability to generate many different ideas in divergent thinking tasks (Bogen & Bogen, 1988; see also Hoppe, 1988).

4.4.3. From Normal via Paranormal to Psychotic Thinking

According to the Swiss psychiatrist and psychologist Eugen Bleuler (see Figure 34)[17], the central symptom in schizophrenia was a pathologically heightened tendency to form associations, what he referred to as a "loosening of associations". Thus, pathological RH semantic processing mechanisms have been hypothesized to underlie schizophrenic patients' disordered thought (e.g., Spitzer, 1993; Spitzer, Braun, Hermle & Maier, 1993). Since neuropsychological experimentation with schizophrenic patients is hampered by the confounds of medication, hospitalization, manifest psychosis (Claridge, Clark & Beech, 1992) as well as psychiatric comorbidity (e.g. polytoxicomania), alternative avenues to the study of the neuropsychiatry of schizophrenia have been developed. One such approach is based on the hypothesis that continuums of psychotic features (i.e., one continuum for each psychotic dimension) exist in the population ranging from healthy to pathological. Thus, also healthy subjects who vary in their degree in which a given psychotic feature is present can be compared

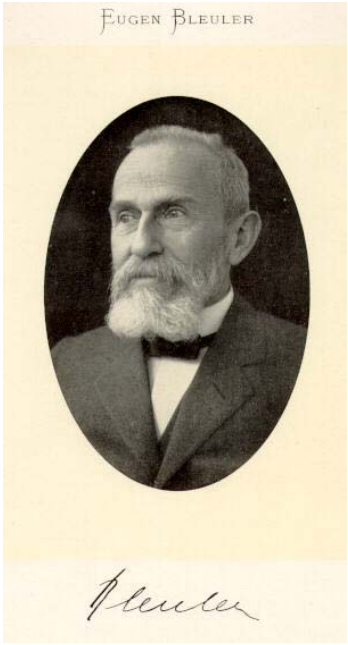


Figure 34. Eugen Bleuler (1857-1939).

[17] Bleuler served as director of the University of Zürich's psychiatric hospital, "Burghölzli", between 1898 and 1927. It was during this time that his seminal paper on schizophrenia, *Dementia Praecox oder Gruppe der Schizophrenien* (1911), was published.

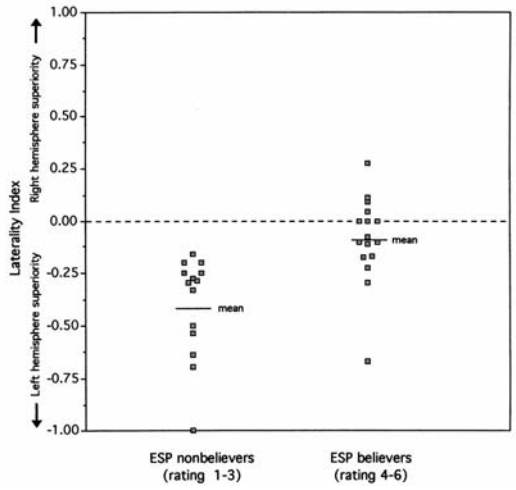


Figure 35. Laterality indices of functional hemispheric superiority for a lexical decision task as a function of belief in ESP (Brugger et al., 1993, p. 1303).

to determine the neuropsychological bases of this psychotic characteristic (Beech & Claridge, 1987). The psychotic feature targeted by Brugger and his coworkers is magical ideation, a symptom central to Schizotypal Personality Disorder (American Psychiatric Association, 1994; see Appendix E). It is typically measured with the Magical Ideation (MI) Scale (Eckblad & Chapman, 1983), a questionnaire which enumerates a number of hallucination-like experiences and delusion-like beliefs (see Appendix F).

The relationship between RH language processing and magical thinking (specifically, belief in extra-sensory perception, or ESP) was investigated in a study by Brugger et al. (1993). These investigators administered healthy, right-handed subjects a bilateral lexical decision task and 6-point scale on which subjects rated their belief in ESP. LH functional hemispheric dominance for this task[18] was greater in disbelievers compared to believers in ESP (see Figure 35). Critically, RVF/LH performances in both groups were comparable; the significant difference in laterality indices originated from believers' superior LVF/RH performances compared to the disbelievers (Brugger, Gamma, Muri, Schafer & Taylor, 1993; see also Leonhard & Brugger, 1998). These findings indicate that a relative overactivity of the RH during lexical language processing underlies magical thinkers' cognitive performance patterns, a finding replicated in groups of high vs. low scorers on the MI scale: high MI scale scorers appreciated more

[18] Functional dominance was measured with laterality indices, i.e., (LVF/RH – RVF/LH) performances / (LVF/RH + RVF/LH) performances.

meaningful connections between randomly paired line drawings (Brugger, Regard, Landis, Krebs & Niederberger, 1994) or randomly paired nouns (Mohr, Graves, Gainotti, Pizzagalli & Brugger, 2001) and generated more “remote” and uncommon associations in spontaneous word generation tasks (Duchêne, Graves & Brugger, 1998) compared to low MI scale scorers.

Structural imaging studies have helped to elucidate the neuroanatomical bases of a relative RH overactivation in individuals with many schizotypal features. For example, reductions in temporal lobe volumes have consistently been reported in schizophrenic subjects (see McCarley, Wible et al., 1999, for a review) which, when asymmetrical, were restricted to the LH (Shenton, Kikinis et al., 1992; Hirayasu, Shenton et al., 1998). Left superior temporal gyral volume reduction has also been related to the degree of thought disorder (Shenton et al., 1992) and has been found in schizotypal personality

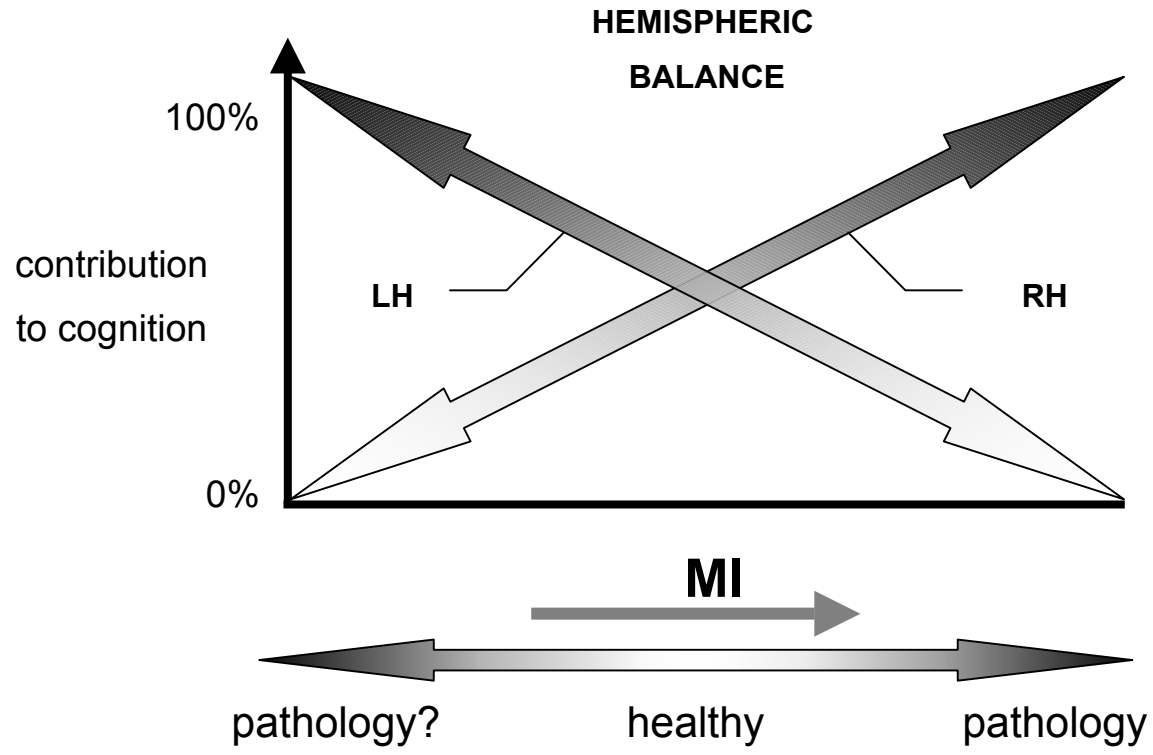


Figure 36. A hemispheric imbalance model of paranormal and psychotic thought (see Leonhard & Brugger, 1998, and Taylor et al., 2002, for reviews).

disordered participants who had neither been medicated nor hospitalized (Dickey, McCarley et al., 1999). Decreased LH capacity, whether genetic (Crow, 1997) or perinatal (Bracha, 1991) in origin, would lead to a functional hemispheric imbalance, i.e. an increased reliance on right hemispheric processing mechanisms (see Figure 36 and Crow, 1997and Leonhard & Brugger, 1998, for reviews). The RH's characteristic widespread activation of the semantic network and coactivation of more distantly related concepts may thus facilitate the formation of delusional ideas and abnormal associations central to psychotic thought (see also Leonhard & Brugger, 1998, and Taylor, Zäch & Brugger, 2002).

4.5. Conclusion

The determination of which aspects of language are in the "right" hemisphere is a complex issue. It depends on a constellation of parameters including both quantitative features of language, i.e. the component language process, the time-course of processing, employed stimulus material and methodological parameters (e.g. priming vs. non-priming, central vs. bilateral vs. unilateral displays in divided visual field paradigms) as well as qualitative aspects of language processing, such as task demands. The present studies attempted to elucidate the parameters under which the RH demonstrates its language, in particular semantic, competence. The ultimate theoretical goal is to describe the interplay between the hemispheres while they store and process semantic information. This goal is fundamental to conceptions of how we store and use knowledge and to our understanding of functional lateralization of the human brain.

5. References

Abernethy, M. and Coney, J. (1993). Associative priming in the hemispheres as a function of SOA. *Neuropsychologia* **31**: 1397-1409.

Abernethy, M. and Coney, J. (1996). Semantic category priming in the left cerebral hemisphere. *Neuropsychologia* **34**: 339-350.

Albert, M. L. (1998). Treatment of Aphasia. *Archives of Neurology* **55**: 1417-9.

Anaki, D., Faust, M. and Kravetz, S. (1998). Cerebral hemispheric asymmetries in processing lexical metaphors. *Neuropsychologia* **36**: 353-362.

Association, A. P. (1994). *Diagnostic and Statistical Manual of Mental Disorders*. Washington, DC, Author.

Atchley, R. A., Keeney, M. and Burgess, C. (1999). Cerebral hemispheric mechanisms linking ambiguous word meaning retrieval and creativity. *Brain and Cognition* **40**: 479-499.

Baayen and al., e. (1995). *The CELEX Lexical Database (CD-ROM)*. Philadelphia, Linguistic Data Consortium, University of Pennsylvania.

Babkoff, H. and Faust, M. (1988). Lexical decision and visual hemifield: An examination of the *RT*-accuracy relationship. *Neuropsychologia* **26**: 711-25.

Balota, D. A. (1994). Visual word recognition: The journey from features to meaning. In M. A. Gernsbacher. *Handbook of Psycholinguistics*. San Diego, Academic Press**:** 303-358.

Baschek, I.-L., Bredenkamp, J., Oehrle, B. and Wippich, W. (1997). Bestimmung der Bildhaftigkeit (I), Konkretheit (C) und der Bedeutungshaltigkeit (m') von 800 Substantiven. *Zeitschrift für experimentelle und angewandte Psychologie* **24**: 353-396.

Beauregard, M., Chertkow, H., Bub, D., Murtha, S., Dixon, R. and Evans, A. (1997). The neural substrate for concrete, abstract and emotional word lexica: A positron emission tomography study. *Journal of Cognitive Neuroscience* **9**: 441-461.

Beech, A. and Claridge, G. (1987). Individual differences in negative priming: relations with schizotypal personality traits. *British Journal of Psychology* **78**: 349-56.

Beeman, M., Friedman, R. B., Grafman, J., Perez, E., Diamond, S. and Lindsay, M. B. (1994). Summation priming and coarse semantic coding in the right hemisphere. *Journal of Cognitive Neuroscience* **6**: 26-45.

Belin, P., Van Eeckhout, P., Zilbovicius, M., Remy, P., Francois, C., Guillaume, S., Chain, F., Rancurel, G. and Samson, Y. (1996). Recovery from nonfluent aphasia after melodic intonation therapy: a PET study. *Neurology* **47**: 1504-11.

Benson, D. F. and Geschwind, N. (1969). The alexias. In P. J. Vinken and G. W. Bruyn. *Handbook of clinical neurology: Disorders of speech, perception and symbolic behavior*. Amsterdam, North-Holland. **4:** 112-40.

Binder, J. and Price, C. J. (2000). Functional neuroimaging of language. In R. Cabezy and A. Kingstone. *Handbook of Functional Neuroimaging of Cognition*. Cambridge, MA, MIT Press**:** 187-251.

Bogen, J. E. and Bogen, G. M. (1988). Creativity and the corpus callosum. *Psychiatric Clinics of North America* **11**: 293-301.

Boles, D. B. (1990). What bilateral displays do. *Brain and Cognition* **12**: 205-228.

Bottini, G., Corcoran, R., Sterzi, R., Paulesu, E., Schenone, P., Scarpa, P., Frackowiak, R. S. J. and Frith, C. D. (1994). The role of the right hemisphere in the interpretation of figurative aspects of language: A positron emission tomography activation study. *Brain* **117**: 1241-53.

Bracha, H. S. (1991). Etiology of structural asymmetry in schizophrenia: An alternative hypothesis. *Schizophrenia Bulletin* **4**: 551-3.

Bradshaw, J. L. (1989). *Hemispheric Specialization and Psychological Function*. Chichester, John Wiley & Sons.

Bradshaw, J. L. and Nettleton, N. C. (1981). The nature of hemispheric specialization in man. *Behavioral and Brain Sciences* **4**: 51-63.

Brownell, H., Potter, H. H. and Michelow, D. (1984). Sensitivity to lexical denotation and connotation in brain-damaged patients: A double dissociation? *Brain and Language* **22**: 253-65.

Brownell, H. H. (1988). Appreciation of metaphoric and connotative word meaning by brain-damaged patients. In C. Chiarello. *Right Hemisphere Contributions to Lexical Semantics*. Berlin, Springer-Verlag**:** 9-31.

Brownell, H. H., Potter, H. H., Bihrle, A. M. and Gardner, H. (1986). Inference deficits in right brain-damaged patients. *Brain and Language* **27**: 310-21.

Brownell, H. H., Simpson, T. L., Bihrle, A. M., Potter, H. H. and Gardner, H. (1990). Appreciation of metaphoric alternative word meanings by left and right brain-damaged patients. *Neuropsychologia* **28**: 375-83.

Brugger, P., Gamma, A., Müri, R., Schäfer, M. and Taylor, K. I. (1993). Functional hemispheric asymmetry and belief in ESP. *Perceptual and Motor Skills* **77**: 1299-308.

Brugger, P., Regard, M., Landis, T., Krebs, D. and Niederberger, J. (1994). Coincidences: who can say how "meaningful" they are? In E. W. Cook and D. L. Delanoy. *Research in Parapsychology 1991*. Metuchen, Scarecrow Press**:** 94-8.

Büchel, C., Price, C. and Friston, K. (1998). A multimodal language region in the ventral visual pathway. *Nature* **394**: 274-277.

Buchinger, C., Flöel, A., Lohmann, H., Van Randenborgh, J., Henningsen, H. and Knecht, S. (2000). Right hemisphere contribution to metaphor processing in healthy subjects. *Journal of Neurolinguistics* **13**: 276-9.

Burgess, C. and Simpson, G. B. (1988). Cerebral hemispheric mechanisms in the retrieval of ambiguous word meanings. *Brain and Language* **33**: 86-103.

Cacciari, C. and Glucksberg, S. (1995). Imaging idiomatic expressions: literal or figurative meanings? In E.-J. v. d. L. M. Everaert, A. Schenk, R. Schreuder. *Idioms: Structural and Psychological Perspectives*. Hillsdale, Lawrence Erlbaum Associates**:** 43-56.

Calvert, G. A., Brammer, M. J., Morris, R. G., Williams, S. C. R., King, N. and Matthews, P. M. (2000). Using fMRI to study recovery from acquired dysphasia. *Brain and Language* **71**: 391-9.

Campbell, J. J. (2000). Neuropsychiatric assessment. In C. E. Coffey and J. L. Cummings. *Textbook of Geriatric Neuropsychiatry*. Washington, DC, American Psychiatric Press**:** 109-24.

Cao, Y., Vikingstad, E. M., George, P., Johnson, A. F. and Welch, K. M. A. (1999). Cortical language activation in stroke patients recovering from aphasia with functional MRI. *Stroke* **30**: 2331-2340.

Caplan, D. (1995). Issues arising in contemporary studies of disorders of syntactic processing in sentence comprehension in agrammatic patients. *Brain and Language* **50**: 325-38.

Cappa, S. F., Perani, D., Grassi, F., Bressi, S., Alberoni, M., Franceschi, M., Bettinardi, V., Todde, S. and Fazio, F. (1997). A PET follow-up study of recovery after stroke in acute aphasics. *Brain and Language* **56**: 55-67.

Cappa, S. F. and Vallar, G. (1992). The role of the left and right hemispheres in recovery from aphasia. *Aphasiology* **6**: 359-72.

Caramazza, A., Hersh, H. and Torgerson, W. S. (1976). Subjective structures and operations in semantic memory. *Journal of Verbal Learning and Verbal Behavior* **15**: 103-17.

Cardebat, D., Demonet, J. F., Viallard, G., Faure, S., Puel, M. and Celsis, P. (1996). Brain functional profiles in formal and semantic fluency tasks: A SPECT study in normals. *Brain and Language* **52**: 305-13.

Carlsson, I., Wendt, P. E. and Risberg, J. (2000). On the neurobiology of creativity. Differences in frontal activity between high and low creative subjects. *Neuropsychologia* **38**: 873-885.

Carroll, J. D. and Chang, J.-J. (1970). Analysis of individual differences in multidimensional scaling via an n-way generalization of "Eckart-Young" decomposition. *Psychometrika* **35**: 283-319.

Carter, C. C., Botvinick, M. M. and Cohen, J. D. (1999). The contribution of the anterior cingulate cortex to executive processes in cognition. *Reviews in the Neurosciences* **10**: 49-57.

Carter, R. (1999). *Mapping the Mind*. London, Orion Publishing Group.

Channon, S., Daum, I. and Polkey, C. E. (1989). The effects of categorization on verbal memory after temporal lobectomy. *Neuropsychologia* **27**: 777-85.

Chapman, L. J. and Chapman, J. P. (1987). The measurement of handedness. *Brain and Cognition* **6**: 175-83.

Chiarello, C. (1985). Hemisphere dynamics in lexical access: Automatic and controlled priming. *Brain and Language* **26**: 146-72.

Chiarello, C. (1988). Semantic priming in the intact brain: Separate roles for the right and left hemispheres? In C. Chiarello. *Right Hemisphere Contributions to Lexical Semantics*. Berlin, Springer-Verlag**:** 59-69.

Chiarello, C. and Beeman, M., Eds. (1998). *Right Hemisphere Language Comprehension: Perspectives from Cognitive Neuroscience*. New Jersey, Lawrence Erlbaum Associates, Inc.

Chiarello, C., Burgess, C., Richards, L. and Pollock, A. (1990). Semantic and associative priming in the cerebral hemispheres: some words do, some words don't... sometimes, some places. *Brain and Language* **38**: 75-104.

Chiarello, C., Senehi, J. and Nuding, S. (1987). Semantic priming with abstract and concrete words: Differential asymmetry may be postlexical. *Brain and Language* **31**: 43-60.

Christensen, P. R., Guilford, J. J., Merrifield, P. R. and Wilson, R. C. (1970). *Alternate Uses*. Beverly Hills, Sheridan Psychological Services.

Chumbley, J. I. and Balota, D. A. (1984). A word's meaning affects the decision in lexical decision. *Memory & Cognition* **12**: 590-606.

Claridge, G. S., Clark, K. H. and Beech, A. R. (1992). Lateralization of the 'negative priming' effect: Relationships with schizotypy and with gender. *British Journal of Psychiatry* **83**: 13-23.

Cohen, L., Dehaene, S., Naccache, L., Lehéricy, S., Dehaene-Lambertz, G., Hénaff, M.-A. and Michel, F. (2000). The visual word form area: Spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. *Brain* **123**: 291-307.

Collins, A. M. and Loftus, E. F. (1975). A spreading-activation theory of semantic processing. *Psychological Review* **82**: 407-28.

Collins, D. L., Neelin, P., Peters, T. M. and Evans, A. C. (1994). Automatic 3D intersubject registration of MR volumetric data in standardized Talairach space. *Journal of Computer Assisted Tomography* **18**: 192-205.

Collins, M. (1999). Differences in semantic category priming in the left and right cerebral hemispheres under automatic and controlled processing conditions. *Neuropsychologia* **37**: 1071-85.

Coltheart, M. (1980). Deep dyslexia: A right-hemisphere hypothesis. In M. Coltheart, K. Patterson and J. C. Marshall. *Deep Dyslexia*. London, Routledge & Kegan Paul**:** 326-80.

Coltheart, M. (1987). Functional architecture of the language-processing system. In M. Coltheart, G. Sartori and R. Job. *The Cognitive Neuropsychology of Language*. London, Lawrence Erlbaum Associates**:** 1-25.

Coltheart, M., Sartori, G. and Job, R., Eds. (1987). *The Cognitive Neuropsychology of Language*. London, Lawrence Erlbaum Associates.

Cook, N. D. (1986). *The Brain Code: Mechanisms of Information Transfer and the Role of the Corpus Callosum*. New York, Methuen & Co.

Cook, N. D. and Beech, A. R. (1990). The cerebral hemispheres and bilateral neural nets. *International Journal of Neuroscience* **52**: 201-10.

Cook, N. D., Früh, H., Mehr, A., Regard, M. and Landis, T. (1994). Hemispheric cooperation in visuospatial rotations: evidence for a manipulation role for the left hemisphere and a reference role for the right hemisphere. *Brain and Cognition* **25**: 240-9.

Crow, T. J. (1997). Schizophrenia as failure of hemispheric dominance of language. *Trends in Neuroscience* **20**: 339-43.

Davison, M. L. (1983). *Multidimensional Scaling*. New York, John Wily & Sons.

Day, J. (1977). Right-hemisphere language processing in normal right-handers. *Journal of Experimental Psychology: Human Perception and Performance* **3**: 518-28.

de Saint Phalle, N. (1971). Do you like my Brain? Lithograph.

Déjérine, J. (1891). Sur un cas de cécité verbale avec agraphie, suivi d'autopsie. *Comptes Rendus des Séances de la Société de Biologie* **43**: 197-201.

Déjérine, J. (1892). Contribution à l'étude anatomo-pathologique et clinique des différentes variétés de cécité verbale. *Comptes Rendus Hebdomadaires des Séances et Mémoires de la Société de Biologie, Ninth series* **4**: 61-90.

Demonet, J.-F., Celsis, P., Nespoulous, J.-L., Viallard, G., Marc-Vergnes, J.-P. and Rascol, A. (1992). Cerebral blood flow correlates of word monitoring in sentences: influence of semantic incoherence. A SPECT study in normals. *Neuropsychologia* **30**: 1-11.

Démonet, J.-F., Chollet, F., Ramsay, S., Cardebat, D., Nespoulous, J.-L., Wise, R., Rascol, A. and Frackowiak, R. (1992). The anatomy of phonological and semantic processing in normal subjects. *Brain* **115**: 1753-1768.

Dickey, C. C., McCarley, R. W., Voglmaier, M. M., Niznikiewicz, M. A., Seidman, L. J., Hirayasu, Y., Fischer, I., Teh, E. K., Van Rhoads, R., Jakab, M., Kikinis, R., Jolesz, F. A. and Shenton, M. E. (1999). Schizotypal personality disorder and MRI abnormalities of temporal lobe gray matter. *Biological Psychiatry* **45**: 1393-402.

Dirnagl, U., Iadecola, C. and Moskowitz, M. A. (1999). Pathobiology of ischaemic stroke: an integrated view. *Trends in Neurosciences* **22**: 391-7.

Drews, E. (1987). Qualitatively different organizational structures of lexical knowledge in the left and right hemisphere. *Neuropsychologia* **25**: 419-427.

Duchêne, A., Graves, R. E. and Brugger, P. (1998). Schizotypal thinking and associative processing: a response commonality analysis of verbal fluency. *Journal of Psychiatry and Neuroscience* **23**: 56-60.

Eckblad, M. and Chapman, L. J. (1983). Magical ideation as an indicator of schizotypy. *Journal of Consulting and Clinical Psychology* **51**: 215-25.

Everitt, B. (1974). *Cluster Analysis*. London, Heinemann Education Books Ltd.

Faust, M. and Weisper, S. (2000). Understanding metaphoric sentences in the two cerebral hemispheres. *Brain and Cognition* **43**: 186-91.

Fiez, J. A. and Petersen, S. E. (1998). Neuroimaging studies of word reading. *Proceedings of the National Academy of Sciences* **95**: 914-21.

Finger, S. (1994). *Origins of Neuroscience: A History of Explorations into Brain Function*. New York, Oxford University Press.

Finger, S. and Roe, D. (1996). Gustave Dax and the early history of cerebral dominance. *Archives of Neurology* **53**: 806-13.

Foldi, N. S. (1987). Appreciation of pragmatic interpretations of indirect commands: Comparison of right and left hemisphere brain-damaged patients. *Brain and Language* **31**: 88-108.

Frackowiak, R. S., Friston, K. J., Frith, C. D., Dolan, R. J. and Mazziotta, J. C. (1997). The cerebral basis of functional recovery. In R.S.J. Frackowiak, K.J. Friston, C. Frith and R. Dolan. *Human Brain Function*. San Diego, Academic Press**:** 275-299.

Franz, S. I. and Davis, E. F. (1933). Simultaneous reading with both cerebral hemispheres. In *Studies in Cerebral Function, IV*, Publications of the University of California at Los Angeles in Education, Philosophy, and Psychology. **I:** 79-90.

Friston, K. J., Holmes, A. P., Price, C. J., Büchel, C. and Worsley, K. J. (1999). Multisubject fMRI studies and conjunction analyses. *NeuroImage* **10**: 385-96.

Furlan, M., Marchal, G., Viader, F., Derlon, J.-M. and Baron, J.-C. (1996). Spontaneous neurological recovery after stroke and the fate of the ischemic penumbra. *Annals of Neurology* **40**: 216-26.

Galuske, R. A. W., Schlote, W., Bratzke, H. and Singer, W. (2000). Interhemispheric asymmetries of the modular structure in the human temporal cortex. *Science* **289**: 1946-9.

Garavan, H., Kelley, D., Rosen, A., Rao, S. M. and Stein, E. A. (2000). Practice-related functional activation changes in a working memory task. *Microsc Res Tech* **51**: 54-63.

Gardner, H. (1984). *Art, Mind, and Brain: A Cognitive Approach to Creativity*. New York, Basic Books.

Gazzaniga, M. S. (1983). Right hemisphere language following brain bisection. A 20-year perspective. *American Psychologist* **38**: 525-537.

Gazzaniga, M. S., Eliassen, J. C., Nisenson, L., Wessinger, C. M., Fendrich, R. and Baynes, K. (1996). Collaboration between the hemispheres of a callosotomy patient. Emerging right hemisphere speech and the left hemisphere interpreter. *Brain* **119**: 1255-62.

Gazzaniga, M. S., Ivry, R. B. and Mangun, G. R. (1998). *Cognitive Neuroscience - The Biology of the Mind*. New York, WW Norton & Company.

Gazzaniga, M. S. and Sperry, R. W. (1967). Language after section of the cerebral commissures. *Brain* **90**: 131-48.

Geschwind, N. (1965). Disconnection syndromes in animals and man. Part 1. *Brain* **88**: 237-94.

Gibbs, R. W. (1995). Idiomaticity and human cognition. In M. Everaert, E.-J. van der Linden, A. Schenk and R. Schreuder. *Idioms: Structural and Psychological Perspectives*. Hillsdale, Lawrence Erlbaum Associates**:** 97-116.

Glosser, G. and Goodglass, H. (1991). Idiosyncratic word associations following right hemisphere damage. *Journal of Clinical and Experimental Neuropsychology* **13**: 703-10.

Gold, B. T. and Kertesz, A. (2000). Right hemisphere semantic processing of visual words in an aphasic patient: an fMRI study. *Brain and Language* **73**: 456-65.

Gold, M. (1997). The strange case of Shepherd Ivory Franz: An evening with Eran Zaidel, Ph.D. *Alumni News, UCLA Psychology Alumni Association* **Fall**.

Goldenberg, J., Mazursky, D. and Solomon, S. (2001). Structures of the mind and universal music. *Science* **292**: 2433.

Gowers, W. R. (1887). *Lectures on the Diagnosis of Diseases of the Brain*. London, Churchill.

Gross, M. M. (1972). Hemispheric specialization for processing visually presented verbal and spatial stimuli. *Perception & Psychophysics* **12**: 357-63.

Grossman, M. and Wilson, M. (1987). Stimulus categorization by brain-damaged patients. *Brain and Cognition* **6**: 55-71.

Hager, W. and Hasselhorn, M. (1994). *Handbuch deutschsprachiger Wortnormen*. Göttingen, Hogrefe.

Hagoort, P., Brown, C. M. and Swaab, T. Y. (1996). Lexical-semantic event-related potential effects in patients with left hemisphere lesions and aphasia, and patients with right hemisphere lesions without aphasia. *Brain* **119**: 627-49.

Harrington, A. (1987). *Medicine, Mind, and the Double Brain*. Princeton, Princeton University Press.

Hart, J., Kraut, M. A., Kremen, S., Soher, B. and Gordon, B. (2000). Neural substrates of orthographic lexical access as demonstrated by functional brain imaging. *Neuropsychiatry, Neuropsychology, and Behavioral Neurology* **13**: 1-7.

Heiss, W. D. (2000). Ischemic penumbra: evidence from functional imaging in man. *Journal of Cerebral Blood Flow and Metabolism* **20**: 1276-93.

Heiss, W.-D., Karbe, H., Weber-Luxenburger, G., Herholz, K., Kessler, J., Pietrzyk, U. and Pawlik, G. (1997). Speech-induced cerebral metabolic activation reflects recovery from aphasia. *Journal of the Neurological Sciences* **145**: 213-7.

Heiss, W.-D., Kessler, J., Karbe, H., Fink, G. R. and Pawlik, G. (1993). Cerebral glucose metabolism as a predictor of recovery from aphasia in ischemic stroke. *Archives of Neurology* **50**: 958-64.

Heiss, W.-D., Kessler, J., Thiel, A., Ghaemi, M. and Karbe, H. (1999). Differential capacity of left and right hemispheric areas for compensation of poststroke aphasia. *Annals of Neurology* **45**: 430-8.

Hellige, J., Ed. (1983). *Cerebral Hemisphere Asymmetry: Method, Theory and Application*. New York, Praeger.

Henderson, V. W. (1986). Anatomy of posterior pathways in reading: a reassessment. *Brain and Language* **29**: 119-133.

Henderson, V. W., Alexander, M. P. and Naeser, M. A. (1985). Left hemisphere pathways in reading: Inferences from pure alexia without hemianopia. *Neurology* **35**: 962-68.

Hines, D. (1976). Recognition of verbs, abstract nouns and concrete nouns from the left and right visual half-fields. *Neuropsychologia* **14**: 211-6.

Hines, D., Czerwinski, M., Sawyer, P. K. and Dwyer, M. (1986). Automatic semantic priming: Effects of category exemplar level and word association level. *Journal of Experimental Psychology: Human Perception and Performance* **12**: 370-9.

Hirayasu, Y., Shenton, M. E., Salisbury, D. F., Dickey, C. C., Fischer, I. A., Mazzoni, P., Kisler, T., Arakaki, H., Kwon, J. S., Anderson, J. E., Yurgelun-Todd, D., Tohen, M.

and McCarley, R. W. (1998). Lower left temporal lobe MRI volumes in patients with first-episode schizophrenia compared with psychotic patients with first-episode affective disorder and normal subjects. *American Journal of Psychiatry* **155**: 1384-91.

Hoppe, K. D. (1988). Hemispheric specialization and creativity. *Psychiatric Clinics of North America* **11**: 303-15.

Howard, D., Patterson, K., Wise, R., Brown, W. D., Friston, K., Weiller, C. and Frackowiak, R. (1992). The cortical localization of the lexicons: positron emission tomography evidence. *Brain* **115**: 1769-1782.

Incisa della Rocchetta, A. (1986). Classification and recall of pictures after unilateral frontal or temporal lobectomy. *Cortex* **22**: 189-211.

Jackman, M. K. (1985). The recognition of tachistoscopically presented words, varying in imagery, part of speech and word frequency, in the left and right visual fields. *British Journal of Psychology* **76**: 59-74.

Jackson, J. H. (1873). On the anatomical and physiological localisation of movements in the brain. *Lancet* **1**: 84-5, 162-4.

Jackson, J. H. (1874). On the nature of the duality of the brain. *Medical Press and Circular, New Ser.* **17**: 19-21, 41-44, 63-66. (Reprinted in Brain, 38, 1915, 80-103.).

James, C. T. (1975). The role of semantic information in lexical decisions. *Journal of Experimental Psychology: Human Perception and Performance* **104**: 130-6.

Jäncke, L., Mirzazade, S. and Shah, N. J. (1999). Attention modulates activity in the primary and secondary auditory cortex: a functional magnetic resonance imaging study in human subjects. *Neuroscience Letters* **266**: 125-128.

Jastrzembski, J. E. (1981). Multiple meanings, number of related meanings, frequency of occurrence, and the lexicon. *Cognitive Psychology* **13**: 278-305.

Joanette, Y. and Goulet, P. (1986). Criterion-specific reduction of verbal fluency in right brain-damaged right-handers. *Neuropsychologia* **24**: 875-9.

Joanette, Y. and Goulet, P. (1988). Word-naming in right-brain-damaged subjects. In C. Chiarello. *Right Hemisphere Contributions to Lexical Semantics*. Berlin, Springer-Verlag.

Johnson, A. M. (1990). A study of humor and the right hemisphere. *Perceptual and Motor Skills* **70**: 995-1002.

Kircher, T. T. J., Brammer, M., Andreu, N. T., Williams, S. C. R. and McGuire, P. K. (2001). Engagement of right temporal cortex during processing of linguistic context. *Neuropsychologia* **39**: 798-809.

Kiss, G. R., Armstrong, C., Milroy, R. and Piper, J. (1973). An associative thesaurus of English and its computer analysis. In A. J. Aitkin, R. W. Bailey and N. Hamilton-Smith. *The Computer and Literary Studies*. Edinburgh, University Press**:** 153-65.

Koenig, O., Wetzel, C. and Caramazza, A. (1992). Evidence for different types of lexical representations in the cerebral hemispheres. *Cognitive Neuropsychology* **9**: 33-45.

Koivisto, M. (1997). Time course of semantic activation in the cerebral hemispheres. *Neuropsychologia* **35**: 497-504.

Koivisto, M. (1998). Categorical priming in the cerebral hemispheres: automatic in the left hemisphere, postlexical in the right hemisphere? *Neuropsychologia* **36**: 661-8.

Koivisto, M. (1999). Hemispheric dissociations in controlled lexical-semantic processing. *Neuropsychologia* **13**: 488-97.

Koivisto, M. and Hamalainen, H. (2002). Hemispheric semantic priming in the single word presentation task. *Neuropsychologia* **40**: 978-85.

Koivisto, M. and Laine, M. (2000). Hemispheric asymmetries in activation and integration of categorical information. *Laterality* **5**: 1-21.

Kruskal, J. B. and Wish, M. (1978). *Multidimensional Scaling*. Beverly Hills, Sage Publications.

Kuperberg, G. R., McGuire, P. K., Bullmore, E. T., Brammer, M. J., Rabe-Hesketh, S., Wright, I. C., Lythgoe, D. J., Williams, S. C. R. and David, A. S. (2000). Common and distinct neural substrates for pragmatic, semantic, and syntactic processing of spoken sentences: An fMRI study. *Journal of Cognitive Neuroscience* **12**: 321-41.

Lambert, S., Sampaio, E., Scheiber, C. and Mauss, Y. (2002). Neural substrates of animal mental imagery: calcarine sulcus and dorsal pathway involvement - an fMRI study. *Brain Research* **924**: 176-83.

Landis, T. (1987). *Right Hemisphere Reading: A Clinico-Experimental Approach to the Dual Brain Interaction*. Habilitationsschrift, Medizinische Fakultät der Universität Zürich. Zürich, University of Zürich**:** 78.

Landis, T., Regard, M., Graves, R. and Goodglass, H. (1983). Semantic paralexia: A release of right hemispheric function from left hemispheric control? *Neuropsychologia* **21**: 359-64.

Landis, T., Regard, M. and Serrat, A. (1980). Iconic reading in a case of alexia without agraphia caused by a brain tumor: a tachistoscopic study. *Brain and Language* **11**: 45-53.

Leonhard, D. and Brugger, P. (1998). Creative, paranormal, and delusional thought: A consequence of right hemisphere semantic activation? *Neuropsychiatry, Neuropsychology, and Behavioral Neurology* **11**: 177-83.

Mannhaupt, H.-R. (1983). Produktionsnormen für verbale Reaktionen zu 40 geläufigen Kategorien. *Sprache und Kognition* **4**: 264-278.

Marchal, G., Benali, K., Iglesias, S., Viader, F., Derlon, J.-M. and Baron, J.-C. (1999). Voxel-based mapping of irreversible ischaemic damage with PET in acute stroke. *Brain* **123**: 2387-400.

Marshall, J. C. and Patterson, K. E. (1983). Semantic paralexia and the wrong hemisphere: a note on Landis, Regard, Graves and Goodglass (1983). *Neuropsychologia* **21**: 425-7.

Martin, R. C., Loring, D. W., Meador, K. J. and Lee, G. P. (1990). The effects of lateralized temporal lobe dysfunction on formal and semantic word fluency. *Neuropsychologia* **28**: 823-9.

Martin-Loeches, M., Hinojosa, J. A., Fernandez-Frias, C. and Rubia, F. J. (2001). Functional differences in the semantic processing of concrete and abstract words. *Neuropsychologia* **39**: 1086-96.

Martindale, C., Hines, D., Mitchell, L. and Covello, E. (1984). EEG alpha asymmetry and creativity. *Personality and Individual Differences* **5**: 77-86.

McCarley, R. W., Wible, C. G., Frumin, M., Hirayasu, Y., Levitt, J. J., Fischer, I. A. and Shenton, M. E. (1999). MRI anatomy of schizophrenia. *Biological Psychiatry* **45**: 1099-119.

McDonald, S. (1993). Viewing the brain sideways? Frontal versus right hemisphere explanations of non-aphasic language disorders. *Aphasiology* **7**: 535-49.

McMullen, P. A. and Bryden, M. P. (1987). The effects of word imageability and frequency on hemispheric asymmetry in lexical decisions. *Brain and Language* **31**: 11-25.

Mednick, S. A. (1962). The associative basis of the creative process. *Psychological Review* **69**: 220.32.

Mednick, S. A. and Mednick, M. T. (1967). *Remote Associates Test: Examiners Manual*. Boston, Houghton-Mifflin.

Meier, E. (2002). *Hemisphärische Unterschiede bei der Verarbeitung von Wörtern mit konnotativer Bedeutung*. Lizentiatsarbeit der Philosophischen I Fakultät der Universität Zürich. Zürich, University of Zürich.

Merriam-Webster, I. (1998). *Merriam Webster's Collegiate Dictionary*. Springfield, Author.

Meyer, D. E. and Schvaneveldt, R. W. (1971). Facilitation in recognizing pairs of words: Evidence of a dependence between retrieval operations. *Journal of Experimental Psychology* **90**: 227-34.

Mimura, M., Kato, M., Kato, M., Sano, Y., Kojima, T., Naeser, M. and Kashima, H. (1998). Prospective and retrospective studies of recovery in aphasia: Changes in cerebral blood flow and language functions. *Brain* **121**: 2083-2094.

Min Kang, A., Constable, R. T., Gore, J. C. and Avrutin, S. (1999). An event-related fMRI study of implicit phrase-level syntactic and semantic processing. *NeuroImage* **10**: 555-61.

Mishkin, M. and Forgays, D. G. (1952). Word recognition as a function of retinal locus. *Journal of Experimental Psychology* **43**: 43-8.

Mohr, B., Pulvermüller, F., Rayman, J. and Zaidel, E. (1994). Interhemispheric cooperation during lexical processing is mediated by the corpus callosum: evidence from the split-brain. *Neuroscience Letters* **181**: 17-21.

Mohr, C., Graves, R. E., Gainotti, L. R. R., Pizzagalli, D. and Brugger, P. (2001). Loose but normal: a semantic association study. *Journal of Psycholinguistic Research* **30**: 475-83.

Moore, C. J. and Price, C. J. (1999). Three distinct ventral occipitotemporal regions for reading and object naming. *NeuroImage* **10**: 181-92.

Moscovitch, M. (1986). Afferent and efferent models of visual perceptual asymmetries: theoretical and empirical implications. *Neuropsychologia* **24**: 91-114.

Moss, H. E., Ostrin, R. K., Tyler, L. K. and Marslen-Wilson, W. D. (1995). Accessing different types of lexical semantic information: Evidence from priming. *Journal of Experimental Psychology: Learning, Memory, and Cognition* **21**: 863-83.

Mummery, C. J., Patterson, K., Hodges, J. R. and Price, C. J. (1998). Functional neuroanatomy of the semantic system: divisible by what? *Journal of Cognitive Neuroscience* **10**: 766-77.

Musso, M., Weiller, C., Kiebel, S., Müller, S. P., Bülau, P. and Rijntjes, M. (1999). Training-induced brain plasticity in aphasia. *Brain* **122**: 1781-1790.

Neely, J. H. (1976). Semantic priming and retrieval from lexical memory: Evidence for facilitatory and inhibitory processes. *Memory and Cognition* **106**: 226-54.

Nobre, A. C., Allison, T. and McCarthy, G. (1994). Word recognition in the human inferior temporal lobe. *Nature* **372**: 260-3.

Norman, D. A. and Bobrow, D. G. (1975). On data-limited and resource-limited processes. *Cognitive Psychology* **7**: 44-64.

Nudo, R. J., Wise, B. M., SiFuentes, F. and Milliken, G. W. (1996). Neural substrates for the effects of rehabilitative training on motor recovery after ischemic infarct. *Science* **272**: 1791-4.

Ohyama, M., Senda, M., Kitamura, S., Ishii, K., Mishina, M. and Terashi, A. (1996). Role of the nondominant hemisphere and undamaged area during word repetition in poststroke aphasics: a PET activation study. *Stroke* **27**: 897-903.

Olk, B. and Hartje, W. (2001). The bilateral effect: callosal inhibition or intrahemispheric competition? *Brain and Cognition* **45**: 317-24.

Orgass, B. (1982). Deutsche Bearbeitung des Token-Tests. In E. von De Renzi and L. A. Vignolo. Weinheim, Beltz-Test-Verlag.

Paivio, A., Yuille, J. C. and Madigan, S. (1968). Concreteness, imagery, and meaningfulness values for 925 nouns. *Journal of Experimental Psychology, Monograph Supplement* **76**: 1-25.

Pizzamiglio, L., Galati, G. and Committeri, G. (2001). The contribution of functional neuroimaging to recovery after brain damage: a review. *Cortex* **37**: 11-31.

Poldrack, R. A., Wagner, A. D., Prull, M. W., Desmond, J. E., Glover, G. H. and Gabrieli, J. D. E. (1999). Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *NeuroImage* **10**: 15-35.

Poreh, A. M., Whitman, D. R. and Ross, T. P. (1993-4). Creative thinking abilities and hemispheric asymmetry in schizotypal college students. *Current Psychology: Developmental, Learning, Personality, Social* **12**: 344-52.

Posner, M. I. and Snyder, C. R. R. (1975). Facilitation and inhibition in the processing of signals. In P. M. A. Rabbitt and S. Dornic. *Attention and Performance V*. New York, Academic Press. 669-682.

Price, C., Indefrey, P. and van Turennout, M. (1999). The neural architecture underlying the processing of written and spoken word forms. In C. M. Brown and P. Hagoort. *The Neurocognition of Language*. Oxford, Oxford University Press**:** 211-40.

Price, C. J. (1998). The functional anatomy of word comprehension and production. *Trends in Cognitive Science* **2**: 281-288.

Price, C. J., Moore, C. J., Humphreys, G. W. and Wise, R. J. S. (1997). Segregating semantic from phonological processes during reading. *Journal of Cognitive Neuroscience* **9**: 727-733.

Price, C. J., Wise, R. J. S. and Frackowiak, R. S. J. (1996). Demonstrating the implicit processing of visually presented words and pseudowords. *Cerebral Cortex* **6**: 62-70.

Price, C. J., Wise, R. J. S., Watson, J. D. G., Patterson, K., Howard, D. and Frackowiak, R. S. J. (1994). Brain activity during reading: the effects of exposure duration and task. *Brain* **117**: 1255-1269.

Pugh, K. R., Shaywitz, B. A., Shaywitz, S. E., Constable, R. T., Skudlarski, P., Fulbright, R. K., Bronen, R. A., Shankweiler, D. P., Katz, L., Fletcher, J. M. and Gore, J. C. (1996). Cerebral organization of component processes in reading. *Brain* **119**: 1221-1238.

Pynte, J., Besson, M., Robichon, F.-H. and Poli, J. (1996). The time-course of metaphor comprehension: an event-related potential study. *Brain and Language* **55**: 293-316.

Raichle, M. E., Fiez, J. A., Videen, T. O., MacLeod, A. M., Pardo, J. V., Fox, P. T. and Petersen, S. E. (1994). Practice-related changes in human brain functional anatomy during nonmotor learning. *Cerebral Cortex* **4**: 8-26.

Regard, M., Cook, N., Wieser, H. G. and Landis, T. (1994). The dynamics of cerebral dominance during unilateral limbic seizures. *Brain* **117**: 91-104.

Regard, M. and Landis, T. (1984). Experimentally induced semantic paralexias in normals: a property of the right hemisphere. *Cortex* **20**: 263-70.

Regard, M., Landis, T. and Graves, R. (1985). Dissociated hemispheric superiorities for reading stenography vs print. *Neuropsychologia* **23**: 431-5.

Regard, M., Landis, T. and Hess, K. (1985). Preserved stenography reading in a patient with pure alexia. A model for dissociated reading processes. *Archives of Neurology* **42**: 400-2.

Regard, M., Landis, T., Wieser, H. G. and Hailemariam, S. (1985). Functional inhibition and release: unilateral tachistoscopic performance and stereoelectroencephalographic activity in a case with left limbic status epilepticus. *Neuropsychologia* **23**: 575-81.

Reicher, G. M. (1969). Perceptual recognition as a function of meaningfulness of stimulus material. *Journal of Experimental Psychology* **81**: 275-80.

Richards, L. and Chiarello, C. (1995). Depth of associated activation in the cerebral hemispheres: Mediated versus direct priming. *Neuropsychologia* **33**: 171-9.

Rips, L. J., Shoben, E. J. and Smith, E. E. (1973). Semantic distance and the verification of semantic relations. *Journal of Verbal Learning and Verbal Behavior* **12**: 1-20.

Rodel, M., Cook, N. D., Regard, M. and Landis, T. (1992). Hemispheric dissociation in judging semantic relations: complementarity for close and distant associates. *Brain and Language* **43**: 448-59.

Rumsey, J. M., Horwitz, B., Donohue, B. C., Nace, K., Maisog, J. M. and Andreason, P. (1997). Phonological and orthographic components of word recognition: a PET-rCBF study. *Brain* **120**: 739-759.

Santee, J. L. and Egeth, H. E. (1982). Do reaction time and accuracy measure the same aspects of letter recognition? *Journal of Experimental Psychology: Human Perception and Performance* **8**: 489-501.

Seger, C. A., Desmond, J. E., Glover, G. E. and Gabrieli, J. D. E. (2000). Functional magnetic resonance imaging evidence for right-hemisphere involvement in processing unusual semantic relationships. *Neuropsychology* **14**: 361-9.

Seghier, M., Lazeyras, F., Momjian, S., Annoni, J. M., de Tribolet, N. and Khateb, A. (2001). Language representation in a patient with a dominant right hemisphere: fMRI evidence for an intrahemispheric reorganisation. *Neuroreport* **12**: 2785-90.

Selnes, O. A. (1999). Recovery from aphasia: activating the "right" hemisphere. *Annals of Neurology* **45**: 419-20.

Semmes, J. (1968). Hemispheric specialization, a possible clue to mechanism. *Neuropsychologia* **6**: 11-26.

Shammi, P. and Stuss, D. T. (1999). Humour appreciation: a role of the right frontal lobe. *Brain* **122**: 657-66.

Shenton, M. E., Kikinis, R., Jolesz, F. A., Pollak, S. D., Lemay, M., Wible, C. G., Hokama, H., Martin, J., Metcalf, D., Coleman, M. and McCarley, R. W. (1992). Abnormalities of the left temporal lobe and thought disorder in schizophrenia. *The New England Journal of Medicine* **327**: 604-12.

Shibahara, N. and Lucero-Wagoner, B. (2002). Hemispheric asymmetry in accessing word meanings: concrete and abstract nouns. *Perceptual and Motor Skills* **94**: 1292-300.

Silvestrini, M., Troisi, E., Matteis, M., Cupini, L. M. and Caltagirone, C. (1995). Involvement of the healthy hemisphere in recovery from aphasia and motor deficit in patients with cortical ischemic infarction: A transcranial Doppler study. *Neurology* **45**: 1815-20.

Sparks, R., Helm, N. and Albert, M. (1974). Aphasia rehabilitation resulting from melodic intonation therapy. *Cortex* **10**: 303-16.

Sperry, R. W. (1961). Cerebral organization and behavior. *Science* **133**: 1749-57.

Sperry, R. (1982). Some effects of disconnecting the cerebral hemispheres. *Science* **217**: 1223-6.

Spitzer, M. (1993). Assoziative Netzwerke, formale Denkstörungen und Schizophrenie: Zur experimentellen Psychopathologie sprachabhängiger Denkprozesse. *Nervenarzt* **64**: 147-59.

Spitzer, M., Braun, U., Hermle, L. and Maier, S. (1993). Associative semantic network dysfunction in thought-disordered schizophrenic patients: Direct evidence from indirect semantic priming. *Biological Psychiatry* **34**: 864-77.

Springer, S. P. and Deutsch, G. (1998). *Left Brain, Right Brain: Perspectives from Cognitive Neuroscience*. New York, W.H. Freeman and Co.

Tabossi, P. and Zardon, F. (1995). The activation of idiomatic meaning. In M. Everaert, E.-J. van der Linden, A. Schenk and R. Schreuder. *Idioms: Structural and Psychological Perspectives*. Hillsdale, Lawrence Erlbaum Associates**:** 273-282.

Talairach, J. and Tournoux, P. (1988). *Coplanar Stereotactic Atlas of the Human Brain*. Stuttgart, George Thieme Verlag.

Taylor, K. I., Brugger, P., Weniger, D. and Regard, M. (1999). Qualitative hemispheric differences in semantic category matching. *Brain and Language* **70**: 119-131.

Taylor, K. I., Brugger, P., Weniger, D. and Regard, M. (submitted). The hemisphere's semantic response depends on the question asked. .

Taylor, K. I., Crelier, G., Alkadhi, H., Brugger, P., Kollias, S. and Weniger, D. (submitted). Deconstructing an axiom: A shift to right hemisphere language dominance during pure semantic processing. .

Taylor, K. I., Crelier, G., Alkadhi, H., Brugger, P., Kollias, S. S. and Weniger, D. (2001). An fMRI study of hemispheric competency for lexical and semantic processes in reading. *NeuroImage* **13**: S615 (abstract).

Taylor, K. I., Meier, E., Brugger, P. and Weniger, D. (in press). Right hemispheric competency for idiomatic and metaphoric language. *European Journal of Neuroscience*: (abstract).

Taylor, K. I., Regard, M. and Brugger, P. (1998). Hemispheric differences in semantic category matching. *Journal of the International Neuropsychological Society* **4**: 216 (abstract).

Taylor, K. I., Weniger, D., Regard, M. and Brugger, P. (2000). Task effects on hemispheric differences in semantic processing. *Journal of the International Neuropsychological Society* **6**: 398 (abstract).

Taylor, K. I., Zäch, P. and Brugger, P. (2002). Why is magical ideation related to leftward deviation on an implicit line bisection task? *Cortex* **38**: 247-52.

Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K. and Farah, M. J. (1997). Role of left prefrontal cortex in retrieval of semantic knowledge: a reevaluation. *Proceedings of the National Academy of Sciences* **94**: 14792-7.

Thulborn, K. R., Carpenter, P. A. and Just, M. A. (1999). Plasticity of language-related brain function during recovery from stroke. *Stroke* **30**: 749-754.

Tompkins, C. A., Boada, R. and McGarry, K. (1992). The access and processing of familiar idioms by brain-damaged and normally aging adults. *Journal of Speech and Hearing Research* **35**: 626-37.

Urcuioli, P. J., Klein, R. M. and Day, J. (1981). Hemispheric differences in semantic processing: Category matching is not the same as category membership. *Perception & Psychophysics* **29**: 343-351.

Van Lancker, D. and Cummings, J. L. (1999). Expletives: neurolinguistic and neurobehavioral perspectives on swearing. *Brain Research Reviews* **31**: 83-104.

Van Lancker, D. R. (1987). Comprehension of familiar phrases by left- but not by right-hemisphere damaged patients. *Brain and Language* **32**: 265-77.

Van Orden, G. C., Jansen op de Haar, M. A. and Bosman, A. M. T. (1997). Complex dynamic systems also predict dissociations, but they do not reduce to autonomous components. In A. Caramazza. *Access of Phonological and Orthographic Lexical Forms: Evidence from Dissociations in Reading and Spelling*. Hove, Psychology Press**:** 131-166.

Van Orden, G. C., Johnston, J. C. and Hale, B. L. (1988). Word identification in reading proceeds from spelling to sound to meaning. *Journal of Experimental Psychology: Learning, Memory, and Cognition* **14**: 371-86.

Vandenberghe, R., Price, C., Wise, R., Josephs, O. and Frackowiak, R. S. J. (1996). Functional anatomy of a common semantic system for words and pictures. *Nature* **383**: 254-6.

Varley, R. (1995). Lexical-semantic deficits following right-hemisphere damage: evidence from verbal fluency tasks. *European Journal of Disorders of Communication* **30**: 362-71.

Villardita, C., Grioli, S. and Quattropani, M. C. (1988). Concreteness/abstractness of stimulus-words and semantic clustering in right brain-damaged patients. *Cortex* **24**: 563-71.

Wallach, M. A. and Kogan, N. (1965). *Modes of thinking in young children*. New York, Holt, Rinehart & Winston.

Wapner, W., Hamby, S. and Gardner, H. (1981). The role of the right hemisphere in the appreciation of complex linguistic materials. *Brain and Language* **14**: 15-33.

Warburton, E., Price, C. J., Swinburn, K. and Wise, R. J. S. (1999). Mechanisms of recovery from aphasia: evidence from positron emission tomography studies. *Journal of Neurology, Neurosurgery, and Psychiatry* **66**: 155-161.

Warburton, E., Wise, R. J. S., Price, C. J., Weiller, C., Hadar, U., Ramsay, S. and Frackowiak, R. S. J. (1996). Noun and verb retrieval by normal subjects: Studies with PET. *Brain* **119**: 159-179.

Warrington, E. K. (1975). The selective impairment of semantic memory. *Quarterly Journal of Experimental Psychology* **27**: 635-57.

Weiller, C. (1998). Imaging recovery from stroke. *Experimental Brain Research* **123**: 13-17.

Weiller, C., Isensee, C., Rijntjes, M., Huber, W., Müller, S., Bier, D., Dutschka, K., Woods, R. P., Noth, J. and Diener, H. C. (1995). Recovery from Wernicke's aphasia: a positron emission tomographic study. *Annals of Neurology* **37**: 723-32.

Weinstein, S. and Graves, R. E. (2001). Creativity, schizotypy, and laterality. *Cognitive Neuropsychiatry* **6**: 131-46.

Weinstein, S. and Graves, R. E. (2002). Are creativity and schizotypy products of a right hemisphere bias? *Brain and Cognition* **49**: 138-51.

Weniger, D. and Springer, L. (2002). Therapie der Aphasien. In W. Hartje and K. Poeck. *Klinische Neuropsychologie*. Stuttgart, Thieme**:** 161-73.

Wernicke, C. (1874). *Der aphasische Symptomenkomplex: eine psychologische Studie auf anatomischer Basis*. Breslau, Cohn and Weigert.

Wey, T. V., Cook, N. D., Landis, T., Regard, M. and Graves, R. E. (1993). Lateralized lexical decisions and the effects of hemifield masks: A study of interhemispheric inhibition and release. *International Journal of Neuroscience* **71**: 37-44.

Weylman, S. T., Brownell, H. H., Roman, M. and Gardner, H. (1989). Appreciation of indirect requests by left- and right-brain-damaged patients: the effects of verbal context and conventionality of wording. *Brain and Language* **36**: 580-91.

Winner, E., Brownell, H., Happe, F., Blum, A. and Pincus, D. (1998). Distinguishing lies from jokes: Theory of mind deficits and discourse interpretation in right hemisphere brain-damaged patients. *Brain and Language* **62**: 89-106.

Winner, E. and Gardner, H. (1977). The comprehension of metaphor in brain-damaged patients. *Brain* **100**: 717-29.

Wise, R. J. S., Howard, D., Mummery, C. J., Fletcher, P., Leff, A., Büchel, C. and Scott, S. K. (2000). Noun imageability and the temporal lobes. *Neuropsychologia* **38**: 985-994.

Woods, R. P., Grafton, S. T., Watson, J. D., Sicotte, N. L. and Mazziota, J. C. (1998). Automated image registration: II. Intersubject validation of linear and nonlinear models. *Journal of Computer Assisted Tomography* **22**: 153-65.

Woodward, S. H. (1988). An anatomical model of hemispheric asymmetry. *Journal of Clinical and Experimental Neuropsychology* **10**: 68.

Worsley, K. J., Marrett, S., Neelin, P., Vandal, A. C., Friston, K. J. and Evans, A. C. (1996). A unified statistical approach for determining significant signals in images of cerebral activity. *Human Brain Mapping* **4**: 58-73.

Worsley, K. J., Poline, J. B., Friston, K. J. and Evans, A. C. (1997). Characterizing the response of PET and fMRI data using multivariate linear models. *NeuroImage* **6**: 305-19.

Zahn, R., Huber, W., Drews, E., Erberich, S., Krings, T., Willmes, K. and Schwarz, M. (2000). Hemispheric lateralization at different levels of human auditory word

processing: a functional magnetic resonance imaging study. *Neuroscience Letters* **287**: 195-198.

Zaidel, E. (1978). Auditory language comprehension in the right hemisphere following cerebral commissurotomy and hemispherectomy: A comparison with child language and aphasia. In A. Caramazza and E. B. Zurif. *Language Acquisition and Language Breakdown: Parallels and Divergencies*. Baltimore, Johns Hopkins University Press**:** 229-275.

Zaidel, E. (1982). Reading in the disconnected right hemisphere: An aphasiological perspective. In Y. Zotterman. *Dyslexia: Neuronal Cognitive and Linguistic Aspects*. Oxford, Pergamon Press**:** 67-91.

Zaidel, E. (1983). Disconnection syndrome as a model for laterality effects in the normal brain. In J. Hellige. *Cerebral Hemisphere Asymmetry: Method, Theory and Application*. New York, Praeger**:** 95-151.

Zaidel, E., Kasher, A., Soroker, N., Batori, G., Giora, R. and Graves, D. (2000). Hemispheric contributions to pragmatics. *Brain and Cognition* **43**: 438-43.

Zaidel, E., White, H., Sakurai, E. and Banks, W. (1988). Hemispheric locus of lexical congruity effects: Neuropsychological reeintrepretation of psycholinguistic results. In C. Chiarello. *Right Hemisphere Contributions to Lexical Semantics*. Berlin, Springer-Verlag**:** 71-88.

6. Appendices

Appendix A. Handedness Inventory (Chapman & Chapman, 1987)

Tag Monat Jahr

Vp Num: Untersuchungsdatum: Geburtsdatum: ☐☐☐☐☐☐

Mann / Frau Ausbildung:

Bitte geben Sie an, mit welcher Hand Sie für gewöhnlich folgende Tätigkeiten ausüben (Sie können mit „linke“, „rechte“ oder „beide“ Hände gleichermassen antworten).

Mit welcher Hand....	(3 Pkte)	(1 Pkte)	(2 Pkte)
1) ...zeichnen Sie?	linke	rechte	beide
2) ...schreiben Sie?	linke	rechte	beide
3) ...benutzen Sie einen Flaschenöffner?	linke	rechte	beide
4) ...werfen Sie einen Schneeball, um einen Baum zu treffen?	linke	rechte	beide
5) ...benutzen Sie einen Hammer?	linke	rechte	beide
6) ...eine Zahnbürste?	linke	rechte	beide
7) ...einen Schraubenzieher?	linke	rechte	beide
8) ...einen Radiergummi?	linke	rechte	beide
9) ...einen Tennisschläger?	linke	rechte	beide
10) ...eine Schere?	linke	rechte	beide
11) ...zünden Sie ein Streichholz an?	linke	rechte	beide
12) ...rühren Sie in einer Kelle?	linke	rechte	beide
13) ..Auf welcher Schulter ruht der Schläger beim Baseball o.ä.?	linke	rechte	beide

Total Punkte_____

Familiäre Linkshändigkeit? (Wenn ja, Verwandtschaftsgrad): _____

Appendix B. Target stimulus words employed in the unilateral lexical and semantic decision tasks with English translations.

category	semantic distance: close	semantic distance: distant
clothing:	Bluse - Jupe[19]	Anzug - Helm
	blouse - skirt	*suit - helmet*
	Gürtel - Hose	Hemd - Pelz
	belt - pants	*shirt - fur coat*
	Schal - Mütze	Anorak - Slip
	scarf - cap	*anorak - briefs*
	Schuhe - Socke	Shorts - Frack
	shoes - socks	*shorts – tailcoat*
containers:	Pfanne – Topf	Silo – Vase
	frying pan - pot	*silo - vase*
	Glas – Tasse	Tube – Netz
	glass - cup	*tube - net*
	Mappe – Tasche	Wanne – Sack
	folder - purse	*bathtub - sack*
	Kessel – Eimer	Beutel - Trog
	kettle – bucket	*bag - trough*
fruits and vegetables:	Apfel - Birne	Ananas - Quitte
	apple - pear	*pineapple - quince*
	Bohne - Erbse	Kürbis - Rosine
	beans - peas	*pumpkin - raisin*
	Feige - Dattel	Lauch - Pilz
	fig - dates	*leeks - mushroom*
	Tomate - Gurke	Mandel - Kohl
	tomato - cucumber	*almond - cabbage*
animals:	Katze - Maus	Affe - Ratte
	cat - mouse	*monkey - rat*
	Pferd - Pony	Esel - Luchs
	horse - pony	*jackass - lynx*
	Schaf - Ziege	Hase - Zebra
	sheep - goat	*rabbit - zebra*
	Tiger - Löwe	Wolf - Ochse
	tiger - lion	*wolf - ox*

[19] The French word *jupe* is used in Swiss-German to refer to 'skirt'; in high German, skirt is referred to as *Rock*.

Appendix C. Stimuli employed in funcional MRI study.

Appendix C.1. Task Series 1: Orthographic Task Stimuli

Feature Identification: GO-closed letter (e.g., A, B, D, O, P, Q or R)

- open letter balanced over letter string position (number of stimuli per open letter position: 4-5-4-5-4).
- equal frequency of open letter (i.e., 3 As, Bs, Ds, Ps, Qs and Rs each and 4 Os)
- beginning letter balanced over GO and NOGO stimuli

	CS's with closed letters	CS's without closed letters
1.	**A**FKNL	FTKIS
2.	**B**HSJI	HCXGJ
3.	**D**IFHC	ILUZF
4.	**O**SWTI	JFSYT
5.	M**R**XTL	LJGSE
6.	R**B**JZT	MFNVN
7.	S**D**IKL	RVSXH
8.	T**O**LWC	SUZCM
9.	U**P**NFV	TCMWL
10.	VH**Q**XJ	UZFIG
11.	WL**R**YF	VCNIT
12.	XU**A**CL	WEITF
13.	CL**O**XF	XVJSG
14.	FYI**P**C	CZTJV
15.	HNL**Q**V	FKZFG
16.	IWV**R**C	HXSJU
17.	JSYI**A**L	IFKEV
18.	LJW**D**S	JGMFN
19.	KVCX**O**	LNVFN
20.	NLFI**P**	KMLSI
21.	VTCJ**Q**	NSVCL
22.	CTYJ**B**	VEMFL
23.		CFWGH

Practice Stimuli:

CF**O**KT	UCZSJ
AKTJY	FWNKI

Appendix C.2. Task Series 1: Lexical Task Stimuli

Letter Identification: GO-letter “t”

- all words contained 5 letters and 2 syllables
- the position of target letter “t” balanced over GO stimuli.
- GO words matched in written frequeny to NOGO words (t(21) = 0.088; p = .931).

	with target letter “t”	without target letter "t"
words:		
1.	**T**UMOR	BELAG
2.	**T**ANGO	ESSIG
3.	E**T**HIK	FERSE
4.	S**T**ENO	MÖBEL
5.	S**T**UBE	NAGEL
6.	KA**T**ZE	NEFFE
7.	MO**T**EL	PUPPE
8.	FLÖ**T**E	REGAL
9.	KAN**T**E	SUPPE
10.	KÜS**T**E	VIRUS
11.	PIRA**T**	WIESE
12.	SALA**T**	
consonant strings:		
13.	**T**BNCD	BRCLG
14.	**T**VRWD	VSRSG
15.	C**T**LWL	DRFPM
16.	L**T**NLV	GJZRS
17.	RH**T**MC	KNVDS
18.	DC**T**GN	LFNLP
19.	CL**T**SM	PRKMR
20.	SMN**T**C	PFBNK
21.	LGH**T**F	RKNLC
22.	MDNL**T**	LKRNL
23.	SBRV**T**	PFSWH

Practice Stimuli:

HPBRT	ORKAN
THRON	PBLSF

Appendix C.3. Task Series 1: Semantic Task Stimuli

Meaningfulness: GO-meaningful

Meaningfulness = “Wörter rufen in unterschiedlichem Ausmass andere Wörter (Assoziationen) hervor. Im folgenden sollen Substantive … danach eingestuft werden, in welchem Ausmass sie andere Wörter hervorrufen” (Baschek, Bredenkamp, Oehrle & Wippich, 1997, p. 360).

High and Low Meaningful Stimuli:

- differed with respect to meaningfulness ($t(43) = 6.63$, $p < .0001$)
- did not differ with respect to Imageability ($t(43) = 1.21$, $p = .24$)
- did not differ with respect to written frequency ($t(43) = .90$, $p = .37$)
- did not differ with respect to Concreteness ($t(43) = 1.62$, $p = .11$)
- have a comparable amount of nouns-from verbs (7 and 6 for HI and LO stimuli, respectively)

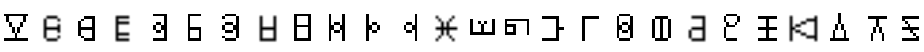
	High Meaningfulness	Low Meaningfulness
1.	NÄHE	SACHE
2.	EXIL	SUCHE
3.	LÜGE	EISEN
4.	SÜNDE	BODEN
5.	TREUE	LARVE
6.	SORGE	ZITAT
7.	LAUNE	THEMA
8.	ÄRGER	ANGABE
9.	FEIER	NUTZEN
10.	GARTEN	EFFEKT
11.	BERUF	SYSTEM
12.	GENUSS	OBJEKT
13.	SEELE	FORMAT
14.	ELEND	DETAIL
15.	ARMUT	HEKTAR
16.	PANIK	ANFANG
17.	TAUFEN	ZUSATZ
18.	WASSER	BETRAG
19.	TEUFEL	PEDANT
20.	PROFIT	ANTEIL
21.	GLAUBE	BEWEIS
22.	GÖTTIN	UNDANK
23.		BEGINN

Practice Stimuli:	GOTT	SEIFE
	WÄRME	FADEN

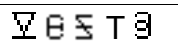
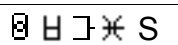
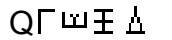
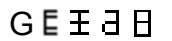
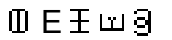
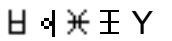
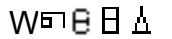
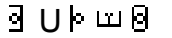
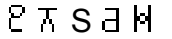
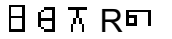
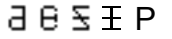
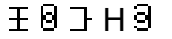
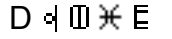
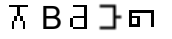
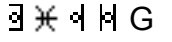
Appendix C.4. Task Series 2: Orthographic Task Stimuli

Scripted Letters: GO-looks like German letter

- False fonts stimuli:

- all stimuli contain five items.
- placement of real letters balanced over GO stimuli (5-4-5-4-5)
- frequency of real letters balanced over GO stimuli

	has a German letter	does not have GL
1.		
2.		
3.		
4.		
5.		
6.		
7.		
8.		
9.		
10.		
11.		
12.		
13.		
14.		
15.		
16.		
17.		
18.		
19.		
20.		
21.		
22.		
23.		

practice stimuli: 

Appendix C.5. Task Series 2: Lexical Task Stimuli

Pseudowords: GO-looks like German word

- all pseudoword stimuli are one-letter variants of real, two-syllabic, five-letter German words
- placement of changed letter balanced over stimuli (4-5-4-5-4)
- Finnish words were selected from Finnish-English dictionary at: http://www.freedict.com/onldict/fin.html.

	Pseudowords	Finnish words
1.	Ligur (**F**igur)	Aivot
2.	Bonat (**M**onat)	Antaa
3.	Wiger (**T**iger)	Hirvi
4.	Rogel (**V**ogel)	Jarru
5.	Apend (A**b**end)	Juuri
6.	Lober (L**e**ber)	Kaari
7.	Nulke (N**e**lke)	Kaksi
8.	Olfer (O**p**fer)	Kehys
9.	Sulbe (S**a**lbe)	Kirja
10.	Frige (Fr**a**ge)	Kuume
11.	Kente (Ke**t**te)	Liina
12.	Mobor (Mo**t**or)	Leoda
13.	Tanel (Ta**f**el)	Muoto
14.	Metur (Met**e**r)	Oikku
15.	Motav (Mot**i**v)	Paeta
16.	Palge (Pal**m**e)	Pohja
17.	Seipe (Sei**d**e)	Poika
18.	Tauke (Tau**b**e)	Putki
19.	Hebet (Hebe**l**)	Sohva
20.	Hotep (Hote**l**)	Sukka
21.	Salab (Sala**t**)	Tyyni
22.	Sirun (Siru**p**)	Uhata
23.		Virhe

Practice Stimuli:

Budel Vihko

Zulpe Yksin

Appendix C.6. Task Series 2: Semantic Task Stimuli

Imageability: GO-high-I

Imageability = “Wörter unterscheiden sich in ihrer Eigenschaft, bildhafte Vorstellungen von Dingen oder Ereignissen hervorzurufen … Im folgenden sollen Substantive … danach eingestuft werden, wie leicht oder schwer sie bildhafte Vorstellungen hervorrufen können” (Baschek, Bredenkamp, Oehrle & Wippich, 1997, p. 357).

High and Low Imageability Stimuli:

- differed with respect to Imageability ($t(43) = 9.45$, $p < .0001$)
- did not differ with respect to Meaningfulness ($t(43) = 1.26$, $p = .21$)
- did not differ with respect to written frequency ($t(43) = 1.38$, $p = .17$)
- differered with respect to Concreteness ($t(43) = 10.46$, $p < .0001$)

	High Imageability	Low Imageability
1.	Gänse	Idee
2.	Gabel	Drama
3.	Allee	Liebe
4.	Nonne	Brise
5.	König	Chaos
6.	Kugel	Ferne
7.	Fahne	Figur
8.	Orkan	Luxus
9.	Altar	Krise
10.	Hafer	Gnade
11.	Sauna	Nässe
12.	Profil	Humor
13.	Butter	Stille
14.	Stange	Kummer
15.	Becher	Besitz
16.	Sänger	Unsinn
17.	Palast	Verein
18.	Papier	Verrat
19.	Panzer	Patent
20.	Wache	Gehalt
21.	Zucker	Winkel
22.	Gitter	Geruch
23.	Klippe	

Practice Stimuli: Blume Stress

Lampe Traum

Appendix C.7. Task Series 3: Orthographic Task Stimuli

Orthographic Decisions: GO-German letter

all stimuli are five-letter strings

	German Consonant Strings	Non-German Letters
1.	Nsgsm	ΩσΔΦσ
2.	Kbzpt	ΘσγσΨ
3.	Brnst	ΩΛΞπΔ
4.	Gnrlt	ΨϑΓσΠ
5.	Rlbtl	ΓΛϑΞλ
6.	Fhltr	ΠλΓςλ
7.	Ntrhl	ΞΨΠλϖ
8.	Mdnng	ΦΞΣςλ
9.	Zgwns	ϑΠΘΣγ
10.	Klpfl	ΣγΛσδ
11.	Brgns	λϕΘΣλ
12.	Stbkz	ΩγσΨσ
13.	Dtslf	ΣΨΔΛΠ
14.	Mttdl	ΔΩςσλ
15.	Rwnht	ΨΠϑΓδ
16.	Frzng	ωϑΦςΨ
17.	Kngrz	ςΠϑγδ
18.	Mnkhc	ΠγΩσζ
19.	Tsndg	ΨΓΛςΣ
20.	Nkrtm	ΣΛΘγδ
21.	Nvlwc	ΔΦΘΞς
22.	Ztlsb	Δϖλ ωΠ
23.		ϑΓΦΩσ

Practice Stimuli:

Pxknf ΨξΔΩϕ

Hlswp Θλσωπ

Appendix C.8. Task Series 3: Lexical Task Stimuli

Lexical Decisions: GO-German word

- all words are five-letter and two-syllabic of roughly equal frequency

	Words	Consonant Strings
1.	Biene	Dbjfy
2.	Euter	Pxssn
3.	Fahne	Ynyrq
4.	Feder	Bhdfk
5.	Flöte	Nykgm
6.	Gerät	Pbwnv
7.	Hafen	Zlcst
8.	Hagel	Btdtr
9.	Hitze	Mhcnf
10.	Käfig	Jxdgw
11.	Kante	Wqgdk
12.	Kehle	Zqgpy
13.	Klima	Dvlfv
14.	Leber	Zmsnw
15.	Mappe	Nxcfb
16.	Magen	Lfbkm
17.	Piste	Rqzjd
18.	Puder	Tlbcg
19.	Rinde	Rxxjh
20.	Sonne	Lzqxs
21.	Tafel	Hhvlp
22.	Tante	Rpkzc
23.	These	

Practice Stimuli:

Notar	Pygcw
Tabak	Cqyrh

Appendix C.9. Task Series 3: Semantic Task Stimuli

Category Membership: GO-fruit/vegetable

- NOGO stimuli comprise all living categories: animals, flowers and trees.
- HI and LOW prototypicality stimuli differed significantly with respect to prototypicality ($t(43) = 14.73$; $p < .0001$)
- GO and NOGO stimuli did not differ with respect to prototypicality ($t(43) = .06$; $p = .95$)
- GO and NOGO stimuli did not differ with respect to written frequency ($t(43) = .83$; $p = .41$)
- HI and LOW prototypicality stimuli did not differ with respect to written frequency ($t(43) = 1.41$; $p = .17$)

	Fruits & Vegetables	Non-Fruits & Non-Vegetables
HI Prototypicality:		
1.	Banane	Nelke
2.	Kirsche	Buche
3.	Pflaume	Elefant
4.	Zitrone	Fichte
5.	Ananas	Aster
6.	Kiwi	Erle
7.	Möhre	Tulpe
8.	Erbse	Birke
9.	Rotkohl	Narzisse
10.	Bohne	Esel
11.	Tomate	Tiger
12.		Maus
LO Prototypicality:		
16.	Quitte	Ferkel
17.	Mandel	Kaktus
18.	Olive	Heide
19.	Gurke	Wicke
20.	Kürbis	Rinde
21.	Beere	Föhre
22.	Dattel	Lamm
23.	Raps	Palme
24.	Pilze	Gazelle
25.	Rübe	Pinie
26.	Mais	Zeder

Practice Stimuli:

Apfel	Rose
Salat	Löwe

Appendix D. Verbal stimuli employed in unilateral category matching experiment.

animals	birds
Affe (monkey)	Ente (duck)
Hund (dog)	Fink (finch)
Löwe (lion)	Gans (goose)
Wolf (wolf)	Rabe (raven)
Katze (cat)	Adler (eagle)
Pferd (horse)	Falke (falcon)
Schaf (sheep)	Meise (titmouse)
Tiger (tiger)	Taube (pigeon)
Elefant (elephant)	Bussard (buzzard)
Schwein (pig)	Papagei (parrot)

Appendix E. Diagnostic Criteria for Schizotypal Personality Disorder (American Psychiatric Association, 1994)

A pervasive pattern of social and interpersonal deficits marked by acute discomfort with, and reduced capacity for, close relationships as well as by cognitive or perceptual distortions and eccentricities of behavior, beginning by early adulthood and present in a variety of contexts, as indicated by five (or more) of the following:

(1) Ideas of reference (excluding delusions of reference)
(2) Odd beliefs or magical thinking that influences behavior and is inconsistent with subcultural norms (e.g., superstitiousness, belief in clairvoyance, telepathy, or „sixth sense“; in children and adolescents, bizarre fantasies or preoccupations)
(3) Unusual perceptual experiences, including bodily illusions
(4) Odd thinking and speech (e.g., vague, circumstantial, metaphorical, overelaborate, or stereotyped)
(5) Suspiciousness or paranoid ideation
(6) Inappropriate or constricted affect
(7) Behavior or appearance that is odd, eccentric, or peculiar
(8) Lack of close friends or confidants other than first-degree relatives
(9) Excessive social anxiety that does not diminish with familiarity and tends to be associated with paranoid fears rather than negative judgments about self.

Appendix F. German version of the Magical Ideation Scale

MI-Skala VP-Nummer:

Bitte beantworten Sie folgende Fragen, indem Sie entweder "stimmt" oder "stimmt nicht" umkreisen.

1) Es gibt Leute, bei denen ich spüre, wenn sie an mich denken	stimmt	stimmt nicht
2) Ich kenne das flüchtige Gefühl, etwas anderes als ein Mensch zu sein	stimmt	stimmt nicht
3) Auf Gehsteigen versuche ich manchmal zu vermeiden, auf Fugen zu treten oder aber die Fugen bewusst nicht zu übergehen	stimmt	stimmt nicht
4) Ich glaube, ich könnte lernen, die Gedanken anderer zu lesen, wenn ich nur wollte	stimmt	stimmt nicht
5) Horoskope sind öfters zutreffend als der Zufall erwarten liesse	stimmt	stimmt nicht
6) Wenn ich nach Hause komme, sind bestimmte Gegenstände manchmal an einem anderen Platz, obschon niemand zugegen war	stimmt	stimmt nicht
7) Zahlen wie „13“ oder „7“ haben keinerlei spezielle Bedeutung für mich	stimmt	stimmt nicht
8) Ich kenne das belustigende Gefühl, Radio- oder TV-Sprecher wüssten, dass ich ihnen zuhörte	stimmt	stimmt nicht
9) Ich war schon mal besorgt darüber, dass Wesen von anderen Planeten Geschehnisse auf der Erde beeinflussen könnten	stimmt	stimmt nicht
10) Die Regierungen halten uns Informationen über UFOs vor	stimmt	stimmt nicht
11) Es ist schon vorgekommen, dass die scheinbar zufällige Anordnung von irgendwelchen Gegenständen mir als Zeichen gedient hat	stimmt	stimmt nicht
12) Ich habe niemals daran gezweifelt, dass Träume das Produkt meiner eigenen Psyche sind	stimmt	stimmt nicht
13) Abgesehen von möglicher Suggestivwirkung, taugen Glücksbringer zu nichts	stimmt	stimmt nicht
14) Beim Anhören von Schallplatten- oder Tonbandaufnahmen habe ich schon Klänge vernommen, die bei anderer Gelegenheit nicht zu hören waren	stimmt	stimmt nicht
15) Scheinbar absichtslose Handbewegungen irgendwelcher Leute haben manchmal einen Einfluss auf mich	stimmt	stimmt nicht
16) Ich träume nie oder fast nie von Ereignissen, die sich erst später ereignen	stimmt	stimmt nicht
17) Ich kenne das Gefühl, dass eine mir bekannte Person vorübergehend druch eine mir femde ersetzt erscheint	stimmt	stimmt nicht
18) Es ist nicht möglich, anderen Leuten zu schaden, indem man lediglich böse Gedanken über sie hegt.	stimmt	stimmt nicht
19) Auch wenn ich alleine bin, fühle ich manchmal die Anwesenheit einer	stimmt	stimmt nicht

Person oder eines fremden Wesens

20) Wenn bestimmte Leute mich ansehen oder mich berühren, habe ich manchmal das Gefühl, Energie zu gewinnen oder zu verlieren	stimmt	stimmt nicht
21) Ich habe manchmal den flüchtigen Gedanken, mir fremde Leute könnten in mich verliebt sein	stimmt	stimmt nicht
22) Ich hatte nie das Gefühl, meine Gedanken würden in Wirklichkeit von jemand anders stammen	stimmt	stimmt nicht
23) Es kommt praktisch nie vor, dass ich das Gefühl habe, eine Person schon zu kennen, wenn diese mir neu vorgestellt wird.	stimmt	stimmt nicht
24) Ich glaube an eine Wiedergeburt	stimmt	stimmt nicht
25) Bisweilen erscheint das Benehmen gewisser Leute so unwirklich, dass man meinen könnte, ihr Auftreten sei inszeniert.	stimmt	stimmt nicht
26) Ich vollziehe ab und zu kleine Rituale, um ungünstige Ereignisse abzuwenden	stimmt	stimmt nicht
27) Ich habe schon befürchtet, ein Geschehnis könnte eintreten, wenn ich ständig an es denke	stimmt	stimmt nicht
28) Ich habe mich schon gefragt, ob die Geister von Verstorbenen einen Einfluss auf uns Lebende haben	stimmt	stimmt nicht
29) Es gab Momente, da habe ich gefühlt, dass eine öffentliche Ansprache oder Vorlesung ganz speziell an mich gerichtet war	stimmt	stimmt nicht
30) Ich habe schon gespürt, wie Fremde meine Gedanken lesen	stimmt	stimmt nicht

Lebenslauf

Kirsten Ingrid Taylor Monsch

Born in Hayward, California, U.S.A. on February 12, 1970.

1976-1978	Sorensen Elementary School, Hayward, California, U.S.A.
1978-1979	Bowman Elementary School, Hayward, California, U.S.A.
1979-1982	Schafer Park Elementary School, Hayward, California, U.S.A.
1982-1984	Grissom Middle School, Mishawaka, Indiana, U.S.A.
1984-1986	Penn High School, South Bend, Indiana, U.S.A.
1986-1987	Aalborghus Gymnasium, Aalborg, Denmark
1987-1988	Penn High School, South Bend, Indiana, U.S.A.
	High School Diploma
1988-1993	University of California at San Diego, La Jolla, California, U.S.A.
	Bachelor of Sciences, Applied Mechanics and Engineering Sciences
	Bachelor of Arts, Psychology
1991-1993	Research Technician, Neuropsychology Laboratory of Prof. Nelson Butters, Veterans Affairs Medical Center, La Jolla, California, U.S.A.
1993-1995	Psychometrist under direction of Profs. Nelson Butters and David Salmon, Alzheimer's Disease Research Center, La Jolla, California, U.S.A.
1995-1999	Faculty of Philosophy I, University of Zürich, Zürich, Switzerland
	Clinical Psychology; minors: 1-adult psychopathology, 2-neuropsychology
	licentiata philosphiae
1999-2002	Assistant at the Neuropsychology Unit (Prof. Dr. phil. M. Regard, director), Neurology Clinic of the University Hospital Zürich, Zürich, Switzerland
	PhD Program in Neurosciences (ETH Zürich and University of Zürich)